1. ADMINISTRATIVE

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Project title: "Improving Understanding of Threats to Whitebark Pine in the Western US: Quantifying Climate Change Effects on Mountain Pine Beetle Outbreaks"

Agreement number: G12AC20481

Date of report: December 20, 2013

Period of time covered by report: October 1, 2012 to December 20, 2013

Actual total cost: $80,484.24 (out of $80,500)

Additional leveraged funding: The project built on the existing collaboration between Hicke and Preisler in which we developed a similar statistical model for mountain pine beetle outbreaks in lodgepole pine forests in Washington and Oregon and published in *Ecology* (Preisler et al. 2012). Our team is developing a similar model in lodgepole pine stands across the West using funding from the USFS Western Wildland Environmental Threat Assessment Center, USGS Climate Research and Development Program through the Western Mountain Initiative, and USDA. We also took advantage of research on increasing understanding of climate/beetle relationships through an empirical analysis of individual outbreaks supported by the USGS and published in *Forest Ecology and Management* (Creeden et al. 2014), which aided in our project.

2. PUBLIC SUMMARY

Whitebark pine is a high-elevation, important tree species that provides critical habitat for wildlife and supplies valued ecosystem services. These trees currently face multiple threats, including attack by mountain pine beetle, which has recently killed whitebark pines over much of the western US. Climate is an important factor in these outbreaks, and future warming is expected to affect epidemics.

Our project developed statistical models of outbreaks in whitebark pine for three regions: the Greater Yellowstone Ecosystem, the Northern US Rocky Mountains, and the Cascade Range. We used these models to understand climate/beetle outbreak relationships, evaluate climatic

causes of recent outbreaks, and estimate the potential for future outbreaks given projections of climate change.

The models fit the observations well, indicating confidence in their reliability. Climate influenced mountain pine beetle outbreaks through fall and winter temperatures, which are direct effects on beetles, as well as via reduced summer precipitation that increase drought stress on trees. Recent outbreaks were caused by warming and drought in the early 2000s. We found that, compared with a baseline of 1985-1994 when little beetle activity occurred, future climate will be more favorable for mountain pine beetle outbreaks in whitebark pine. In the Greater Yellowstone Ecosystem, our preliminary results indicate that some projections were similar to or exceed the climate favorability of conditions during the recent severe and extensive outbreak (2000-2009). Variability existed among outbreak projections as a result of the amount of future warming and changes in precipitation, which are functions of climate model, emissions scenario, and decade.

Our project provides evidence of the importance of climate for influencing recent and future beetle outbreaks in whitebark pine forests. We recommend that land managers and decision makers consider the impacts of expected climate change on mountain pine beetle outbreaks in whitebark pine when planning conservation actions.

3. TECHNICAL SUMMARY

Whitebark pine is a high-elevation, keystone tree species currently subjected to multiple threats, including attack by mountain pine beetle, an aggressive bark beetle that has recently killed whitebark pines over hundreds of thousands of acres in the western US. Climate is an important factor in outbreaks of this beetle through effects on the beetle via warming and on the host tree via stress associated with warming and drought. Future climate change is expected to increase the number, frequency, and/or severity of these epidemics. Our goal was to increase the understanding of the causes of recent mountain pine beetle outbreaks in whitebark pine forests, and to estimate future outbreak potential given future climate change. To accomplish this, we developed empirical models of beetle outbreaks that considered beetle populations, climate, and stand structure. We analyzed generalized additive models of outbreak probability and severity for three separate geographic regions within the range of whitebark pine in the western United States (the Greater Yellowstone Ecosystem, the Northern US Rockies, and the Cascade Range). We used observations from USDA Forest Service aerial surveys to compute the presence of whitebark pine mortality and the number of trees killed by mountain pine beetles within 1-km grid cells, which we used as our response variables. Our explanatory variables were chosen to represent processes affecting mountain pine beetle development and host tree susceptibility based on previous research (Logan and Powell 2001, Carroll et al. 2004, Régnière and Bentz 2007, Aukema et al. 2008, Preisler et al. 2010, Sambaraju et al. 2012), and included climate variables ranging from simple climate variables to outputs of process models of temperature suitability as well as the number of attacking beetles and stand structure.

Our models captured the temporal patterns of observed outbreak area and outbreak severity well in the three regions, indicating confidence in the interpretation and predictions of the models. We found that summer precipitation (drought), winter temperature, and fall temperature were important variables for explaining observed outbreak patterns. The general patterns of climate variable/beetle relationships were similar among regions, although minor differences occurred in the nonlinear forms of some relationships. Our models indicated that the most recent outbreaks were due to a co-occurrence of high fall and winter temperatures that remained favorable during outbreak periods together with intermittent drought.

We performed sensitivity analyses of the regions to expected changes in climate variables by varying one variable at a time. These analyses combined the climate/beetle relationships, the landscape patterns of climate within each region, and the range of expected future change of climate. We found that outbreaks were sensitive to higher winter temperatures in the Greater Yellowstone Ecosystem and to higher fall temperatures in the Cascades and Northern Rockies. A small decrease in summer precipitation (increase in drought) resulted in large increase in outbreaks, and higher summer precipitation (decrease in drought) led to reduced outbreak area and severity.

We estimated future outbreak potential in the Greater Yellowstone Ecosystem using our models applied to downscaled climate change projections from the CMIP5 archive. We selected three general circulation models (GCM) to span a range of warming and changes in summer precipitation. We considered three emissions scenarios and three future decades. Our preliminary results suggest that, compared with a baseline of 1985-1994 in which little beetle activity occurred, future climate will be more favorable for mountain pine beetle outbreaks in whitebark pine. Furthermore, some projections are similar to or exceed the climate suitability during the recent severe and extensive outbreak (2000-2009). Variability existed among projections as a result of the amount of warming, which is a function of GCM, emissions scenario, and decade. Significantly, variability also occurred as a result of the importance of summer drought in our outbreak model and variability in changes of this variable among projections.

Our findings inform land management decisions and US Fish and Wildlife Service considerations of listing whitebark pine as threatened or endangered. Our preliminary results suggest that future climate, including in the near term, may be similar to or more favorable than the climate conditions associated with the highly unusual, extensive, and severe outbreaks that occurred recently. The importance of drought that we found has not, to date, been recognized in this beetle/host system, unlike the role of warming. The uncertainty of precipitation changes with climate projections implies caution when interpreting our results. However, our study suggests that in the absence of any precipitation changes, expected future warming will lead to enhanced weather suitability for mountain pine beetle in whitebark pine forests.

4. PURPOSE AND OBJECTIVES

Whitebark pine (*Pinus albicaulis* Engelm.) is a high-elevation, subalpine tree species that grows throughout much of the western United States. This pine is a foundation and keystone species that provides critical habitat for wildlife (grizzly bears, Clark's nutcrackers), influences soil and snow processes (Tomback et al. 2011), and provides ecosystem services valued by the public (Meldrum et al. 2011). These trees are currently subjected to several threats, including attack by mountain pine beetle (*Dendroctonus ponderosae* Hopkins), white pine blister rust, fire exclusion, and climate change (Tomback et al. 2011). Mountain pine beetles have affected over 100,000 hectares of whitebark pine in the western US in each year from 2007 to 2010 (US Forest Service Aerial Detection Surveys). For these reasons, the US Fish and Wildlife Service (FWS) found that listing whitebark pine as threatened or endangered was warranted but precluded because of higher priority actions (FWS 2011).

The FWS identified climate influences on beetles as a major reason for their finding (FWS 2011). This scientific information was based on the theoretical understanding of individual climate influences and studies of climate suitability of some individual climate processes (Logan and Powell 2001, Logan et al. 2003, Bentz et al. 2010, Logan et al. 2010). Integrated estimates of different influences of climate on beetle outbreaks, estimates of probabilities of beetle outbreak given current climate and scenarios of future climate change, and spatially explicit information quantifying vulnerable locations were not available at that time.

Much is known about the factors that control mountain pine beetle population dynamics and the occurrence of outbreaks in lodgepole pine (*Pinus contorta*) (for reviews, see Raffa et al. 2008, Bentz et al. 2010). Temperature affects beetles through adaptive seasonality and cold tolerance. Adaptive seasonality describes temperature conditions that allow for a one-year life cycle and a synchronized mass emergence of adults in late summer (Logan and Powell 2001). Mountain pine beetle development is strictly controlled by temperature (Logan and Powell 2001), and genetic differences in response to temperature have been found across the beetle's range (Bentz et al. 2001). Cold tolerance describes the probability that beetles will survive the winter. Larvae are the most cold tolerant life stage, but temperatures below -40° C can kill any life stage, and unusually low temperatures during fall and spring can also kill beetles (Wygant 1940, Safranyik and Carroll 2006, Régnière and Bentz 2007).

Drought stress affecting host tree defensive capabilities is another important factor in the occurrence of mountain pine beetle outbreaks. When trees are stressed from lack of water, they are less able to defend themselves against beetle attack (Raffa and Berryman 1983, McDowell et al. 2011). However, severe drought stress can result in thin phloem that does not provide sufficient food resources and that desiccates quickly (Amman 1972, Safranyik and Carroll 2006).

Historically, mountain pine beetle outbreaks were rare in whitebark pine forests. The high-elevation whitebark pine forests have typically been outside the thermal limits of adaptive seasonality and cold tolerance (Logan and Powell 2001, Logan et al. 2010). However, during the 2000s decade, widespread outbreaks were observed in whitebark pine (Gibson 2006). Model predictions have suggested increased temperature suitability for mountain pine beetle outbreaks in recent and future decades (Hicke et al. 2006, Littell et al. 2010, Logan et al. 2010), raising concern about impacts on future abundance and distribution of whitebark pine.

Whitebark pine conservation is of interest in several agencies and institutions. Whitebark pine is specifically identified in an FY12 Great Northern Landscape Conservation Cooperative Funding Guidance (funding opportunity) as a topic of interest. The USDA Forest Service is performing research, management, and restoration activities to promote the conservation of whitebark pine (Goheen and Sniezko 2007, Keane et al. 2011). The Greater Yellowstone Coordinating Committee, Whitebark Pine Subcommittee and the General Management Plan of Glacier National Park address whitebark pine threats (Greater Yellowstone Coordinating Committee Whitebark Pine Subcommittee 2011). National Park Service Inventory and Monitoring networks throughout the West (Klamath, Upper Columbia Basin, Greater Yellowstone, Sierra Nevada, North Coast and Cascades) are targeting whitebark pine for inventorying and monitoring.

The original objectives of our project were:

1) develop a statistical model for predicting outbreaks of mountain pine beetle in whitebark pine that considers beetle population phase, stand structure, and climate;
2) evaluate regional differences in the probability of outbreak given current climate;
3) produce predictions of changes in probability of beetle outbreaks in whitebark pine given future scenarios of climate change; and
4) estimate the expected area of damage from beetle outbreaks in present and future climates.

There were no modifications to the original objectives.

5. ORGANIZATION AND APPROACH

5.1 Identify study areas

Populations of mountain pine beetle exhibit different sensitivities to climate (Bentz et al. 2001), so we wanted to allow for such differences in our study by developing different models for different regions. We separated the distribution of whitebark pine in the western US into three major ecoregions to be used in our project (Figure 1): Cascade Range, Northern US Rocky Mountains, and Greater Yellowstone Ecosystem. Other regions within the whitebark pine distribution (e.g., the Sierra Nevada) did not have significant mountain pine beetle outbreaks and/or specific beetle information was not available for these regions.

5.2 Assemble response variables (mortality area and number of trees killed by mountain pine beetles) for statistical analysis

For our large-scale analysis that covered the distribution of whitebark pine in the western US, we required a spatially extensive data set over multiple years that identified whitebark pines killed by mountain pine beetles. We used the only available data set, the Aerial Detection Survey (ADS) database, maintained by the USDA Forest Service. This database contains mountain pine beetle-caused mortality of whitebark pine during 1997–2010. These data were collected by observers in aircraft who recorded the damage agent (e.g., mountain pine beetle), damage severity, and species of damaged trees as polygons on maps, including areas with no observable damage. Meddens et al. (2012) converted these ADS data to 1-km grids of the number of trees killed for each beetle and tree species combination for the western United States. The number of trees killed by mountain pine beetles in whitebark pine in each year was the basis for our response variables. We defined two response variables for statistical analysis: mortality area, which are locations that experienced any amount of whitebark pines killed by mountain pine beetle, and the number of whitebark pines killed by mountain pine beetle. USDA Forest Service Forest Insect and Disease Conditions reports for the Greater Yellowstone Ecosystem stated that beetle outbreaks in the area had declined to very low levels by 1986. Therefore, we added 1985-1995 to our time series, specifying no beetle activity during this period. One-km grids during 1985-2010 were created for each variable in each region.

ADS data identify mountain pine beetle-caused tree mortality based on the presence of red needles. Mountain pine beetles disperse and attack trees in late summer, but the needles do not turn red until the following summer. We therefore defined the year of attack as the year prior to the year reported in the ADS database, and thus our study period was 1985-2009.

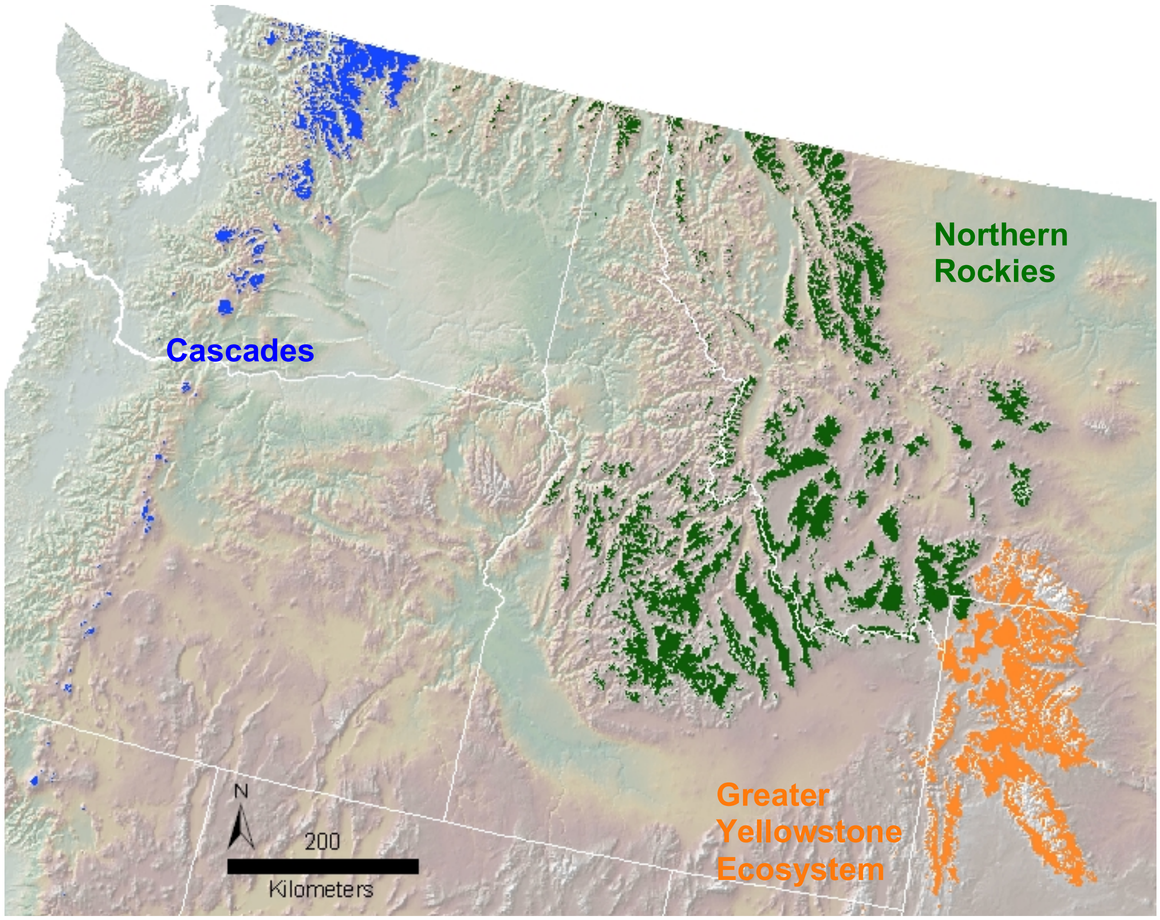

Figure 1. The three geographic regions of our study to model mountain pine beetle outbreaks in whitebark pine forests.

5.3 Assemble explanatory variables (climate, beetle pressure, stand information)

Explanatory variables were chosen to represent known processes that influence mountain pine beetle outbreaks based on previous field, laboratory, and observational studies (Shore and Safranyik 1992, Logan and Powell 2001, Safranyik and Carroll 2006, Bentz et al. 2010). We grouped these variables into three categories representing beetle pressure, weather conditions, and stand characteristics (Table 1). Beetle pressure is the number of beetles attacking a stand in the current year. We represented beetle pressure with two variables: first, a term representing the dispersal of beetles into the focal cell (cell of interest) using the number of trees killed within a neighborhood in the previous year, and second, a term representing attacking beetles that emerged from trees within the focal cell using the number of trees killed in that cell in the previous year.

Climate (weather) variables were selected based on their availability, computational demand (monthly data were easier to use than daily data), and spatial and temporal characteristics (resolution and extent). We used a combination of simple climate variables (e.g., mean annual temperature), more complex climate variables that better represented beetle/host ecological processes (e.g., climatic water deficit), and beetle process model results. Daily climate variables were calculated from daily temperature and precipitation interpolated through inverse distance weighting and vertical lapse rates within the BioSIM program (Régnière et al. 1996). BioSIM was also used to generate annual climate suitability indices of cold tolerance (Régnière and Bentz 2007) and adaptive seasonality (Logan and Powell 2001). Monthly climate variables were calculated from 800-m Parameter-elevation Regressions on Independent Slopes Model (PRISM) data (PRISM Group 2006). Climatic water deficit was computed using the AET calculator program (http://geography.uoregon.edu/envchange/pbl/software.html) with monthly PRISM data.

Variables representing stand conditions were selected on the basis of availability. To include the effects of higher susceptibility of older and larger trees (Shore and Safranyik 1992), we used a 250-m map of forest biomass from Blackard et al. (2008). We also include basal area from the USDA Forest Service National Risk Map (Krist et al. 2007) to represent host susceptibility to beetle attack. The presence of whitebark pine forest, which limited the spatial extent of our study, was determined for the Northern Rockies and Cascades regions from a combination of areas coded as whitebark pine in the ADS data and a map of the potential for blister rust infection. In the Greater Yellowstone Ecosystem, we used a 30-m map of whitebark pine presence developed by Landenburger et al. (2008), which we aggregated to our 1-km grid to compute the percentage whitebark pine within a grid cell. We also used this variable as a potential explanatory variable.

5.4 Determine appropriate statistical methods

We carefully considered the structure of our statistical analysis. We wanted to include nonlinear relationships between outbreaks and explanatory variables because our past research demonstrated this need (Preisler et al. 2012). We also needed to account for the non-normal distribution of the number of trees killed response variable, which contained many more zeros (areas without beetle activity) than outbreak areas. To meet these objectives, we modeled mountain pine beetle outbreaks in a two-step process. First, we modeled the presence of mortality due to mountain pine beetles, and second, we modeled the continuous number of trees killed once at least one tree had been killed.

We modeled the presence of mortality (mortality area) with logistic regression, defined by equation

$$logit(p) = \beta_o + s_{m1}(X_{m1}) + \cdots s_{mi}(X_{mi}) \qquad \text{Eq. 1}$$

where p is the probability of mortality from mountain pine beetles and $s_{m1}(X_{M1})$ through $s_{mi}(X_{Mi})$ are tensor product smooth functions of the explanatory variables. Voxels (grid cells in a given year; x, y, time) were defined as having whitebark pine mortality when at least one tree was killed by mountain pine beetles that year. No-mortality voxels (zeros) were defined as those voxels within the range of whitebark pine that were flown during aerial surveys that had no recorded beetle-killed trees.

For the subset of voxels for which at least one tree was killed in the current year, we modeled the number of trees killed (outbreak severity). To require all explanatory variables be suitable for the continuation of an outbreak, or conversely for one unsuitable explanatory variable to trigger decline, we used a multiplicative model (additive in logarithms) of the form

$$E(Y|\,Y > 0) = \beta_o + s_{m1}(\ln(X_{M1})) + \cdots s_{mi}(\ln(X_{Mi})) \qquad \text{Eq. 2}$$

where *E(Y|Y>0)* is the number of trees killed given that at least one tree has been killed, and $s_{m1}(ln(X_{M1}))$ through $s_{mi}(ln(X_{Mi}))$ are tensor product smooth functions of the natural logarithm of the explanatory variables. Because this model estimates the number of trees killed conditional on at least one tree having been killed, hereafter we refer to this as the conditional model.

To estimate the unconditional number of trees killed, we multiplied the probability of mortality in a given voxel, determined using the logistic regression model (Equation 1), by the conditional number of trees killed (Equation 2). We present results for the probability of mortality and unconditional outbreak severity.

Both the logistic regression and conditional models were constructed as generalized additive models, which allow for nonlinear relationships between response and explanatory variables. We used the mgcv package (Wood 2011) within the R statistical program (R Development Core Team 2010).

We used a model selection process that ranks models with different sets of explanatory variables according to the Akaike Information Criterion (AIC) to determine the variables that best represented each of the processes in Table 1. Because weather variables tend to be correlated, we calculated concurvity (akin to multiple collinearity in a linear model) among variables for the top logistic and conditional model. When concurvity was greater than 0.5, we assessed the effects of removing correlated variables on the smoothing functions of the other variables. When removing variables altered the smoothing functions of the remaining variables, we competed models with only uncorrelated (low concurvity) variables to determine which of the correlated variables to keep. When the jackknife standard errors for a variable (see below for calculation details) included 0 along the entire range of the variable, that variable was dropped from the final model.

We evaluated model goodness-of-fit in several ways. For the logistic model we performed cross-validation by year; that is, we calculated a model with one year of data withheld and then predicted the withheld year with that model. From this we produced a time series of the observed and expected area of mortality. For the conditional model we examined R^2 and RMSE of the predictions relative to the observations.

Because our model parameters did not vary among years, we assessed the significance of individual explanatory variables by calculating jackknife standard errors by year. We developed 12 models (1998-2009, years of beetle activity) each with one year of data withheld at a time and then estimated the response variables of the full data set using that model. Standard errors were calculated from that population of estimates. Significance was determined from visual inspection of the log-odds plots of the logistic regression model coefficients and partial residual plots of the continuous model coefficients (these plots quantify the relationship between an explanatory variable and the response variable while holding other explanatory variables constant). Those variables whose standard errors did not include zero had a conclusive effect on the model prediction. Greater magnitudes of the y-axis on those plots indicate effects of that variable.

5.5 Interpret models and compare models from different geographic regions

We interpreted climate/beetle relationships in several ways. We identified variables important for explaining mortality area and number of trees killed by holding each explanatory variable constant and computing the change in RMSE compared with the observations. We assessed the relationship between explanatory variables and response variables using log-odds and partial residual plots (described above). Finally, we quantified the contribution of individual explanatory variables during the years of outbreaks. We also compared model results among our three different regions by assessing differences in model goodness-of-fit and climate/beetle relationships (log-odds and partial residual plots).

5.6 Assess changes in climate suitability during the last 100 years

We evaluated changes in climate suitability for mountain pine beetle outbreaks in whitebark pine forests by analyzing patterns of climate variables during 1900-2009 (Figures S1-S3) and applying our models to the 1900-2009 time frame using PRISM monthly data. To do this, we set all non-weather variables to their values where the log-odds and partial residuals equal 0 and set weather variables to their observed values. We then estimated mortality area and number of trees killed with the logistic and conditional models, respectively, then multiplied the results to produce the unconditional estimate of the number of trees killed through time. For the logistic model, we plotted the yearly spatial average (across the study region) of the linear predictor (the log-odds of mortality), and for the unconditional model, we plotted the yearly spatial average of the predicted number of trees killed. The resulting variables can be viewed as weather suitability given there are no beetles present on the landscape.

5.7 Assess changes in climate suitability using projections of future climate

We determined the influence of future climate change on mountain pine beetle outbreaks in two ways. First, we ran sensitivity tests in which we varied one climate explanatory variable at a time while holding other variables (including other climate variables) at their observed values and evaluated model predictions. The future range of each explanatory variable was determined by inspection of changes from a suite of climate model projections for the western United States (Rupp et al., in prep.). The relationship between fall and winter temperatures and outbreaks were highly uncertain at the highest temperatures (based on the large standard errors evident in the log-odds and partial residual plots). As a result, we clamped (truncated) future temperature values at the maximum values at which these plots showed standard errors that did not bound zero. This sensitivity analysis combined the log-odds or partial residual plots, which define climate/beetle relationships, with the current spatial and temporal conditions of the explanatory variable of interest within each geographic region. The analysis illustrates how future changes in each climate explanatory variable influence beetle outbreaks in isolation. However, the analysis is unrealistic in the sense that increasing one temperature variable by, say, 5 ºC while holding other temperature variables constant does not represent future conditions.

Second, we applied our models to a suite of climate change projections. Here, we allowed all climate variables to vary as determined by the projections. We began with the suite of general circulation model (GCM)/ensemble projections from the CMIP5 archive that were analyzed by Rupp et al. (2013) for the western US, who evaluated the performance of historical model output for 20 different GCMs. We then considered the top 10 of these GCMs as identified by Rupp et al. (2013). For available ensemble members from each available GCM, Rupp et al. (in prep.) plotted the change in temperature and precipitation in the western US for annual and seasonal time periods, for different emissions pathways, and for different future years. We used annual, December-January-February, and June-July-August time periods for RCP8.5 and means from 2069-2098 for selection. We then selected three GCMs that spanned the range of projections of changes in temperature and precipitation relative to 1970-1999 means. CanESM2 produced warmer and wetter projections, IPSL-CM5A-MR had warmer and drier projections, and CCSM4 projections had less warming than and similar precipitation conditions as today. We used the NASA NEX-DCP30 downscaled CMIP5 database because of availability and because the climate variables we needed are covered by this database. Because the NEX-DCP30 archive only has the first ensemble member for each GCM, we focused on these for our analysis. Climate explanatory variables (e.g., mean April-August temperature) were computed from these downscaled projections for three representative concentration pathways (RCP2.6, 4.5, and 8.5) and for 2020-2029, 2050-2059, and 2090-2099.

We ran the 27 combinations of GCM, RCPs, and decades using our top model for the Greater Yellowstone Ecosystem (results from other regions forthcoming). We held non-climate variables (beetle pressure, stand structure) constant, and therefore we consider the model output a weather suitability index. To avoid extrapolation of relationships between outbreaks and climate variables beyond the ranges of observed climate during recent years, we clamped (truncated) future values of weather variables to their maximum observed values during 1985-2009. This is a slightly different method of clamping than for the sensitivity analyses above; we are working on choosing the best method of clamping that includes the issues of uncertainty and extrapolation, and the selected method will be used in subsequent presentations and publications. We compared annual summed weather suitability distributions within one decade (one value per year) to weather suitability indices during the preoutbreak (1986-1995) and current outbreak (2000-2009) periods.

6. PROJECT RESULTS

6.1 Climate influences on mortality area

In all three regions, our top model of outbreak probability captured the temporal pattern of mortality area well (Figure 2). Both the timing and magnitude of observed mortality area was replicated by our models across all three regions. Spatial patterns of modeled tree mortality in the Greater Yellowstone Ecosystem were similar to observed patterns (Figure 3). Part of this success resulted from our use of beetle pressure variables, which were derived from the number of trees killed in the previous year.

Explanatory variables that we selected to represent the different processes by which climate influenced outbreaks were similar, but not identical, across regions (Figures S4-S6). In the Greater Yellowstone Ecosystem, winter mortality was best represented by cold tolerance (which is related to beetle mortality during the cold season). Because cold tolerance is a computationally expensive variable to calculate, we examined the changes in model performance when we substituted winter minimum temperature (the second best winter mortality variable). Making this substitution did not substantially reduce the model fit, nor alter our interpretation of the other explanatory variables. We therefore used winter minimum temperature in our final model. Outbreak probability increased with increasing winter minimum temperature (Figure S4). Winter mortality was best represented by winter minimum temperature in the Northern Rockies (Figure S5) and the Cascades (Figure S6), where again, increasing temperature led to a greater probability of tree mortality.

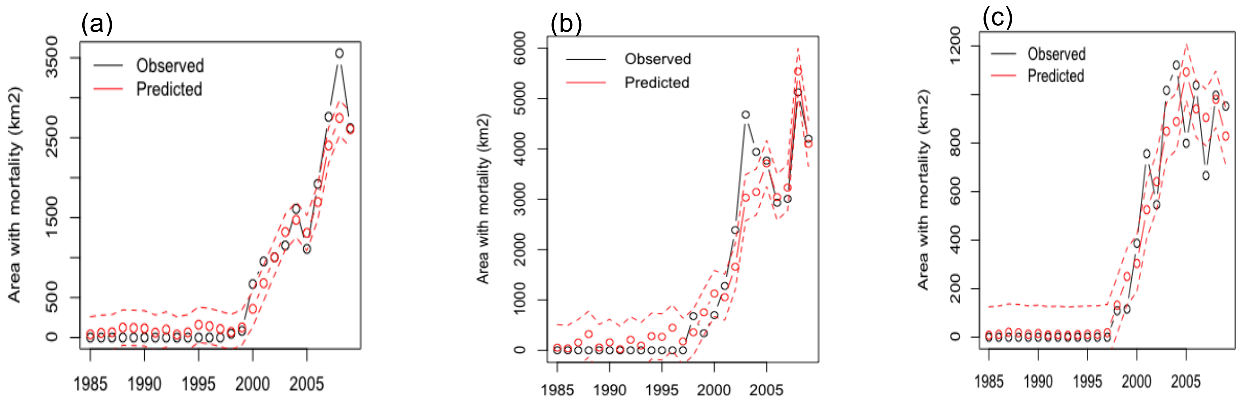

Figure 2. Observed and predicted area of whitebark pine mortality due to mountain pine beetles for the (a) Greater Yellowstone Ecosystem, (b) Northern Rockies, and (c) Cascades regions. Predicted mortality area was calculated by summing the probability of mortality across 1-km grid cells for each year in the study area.

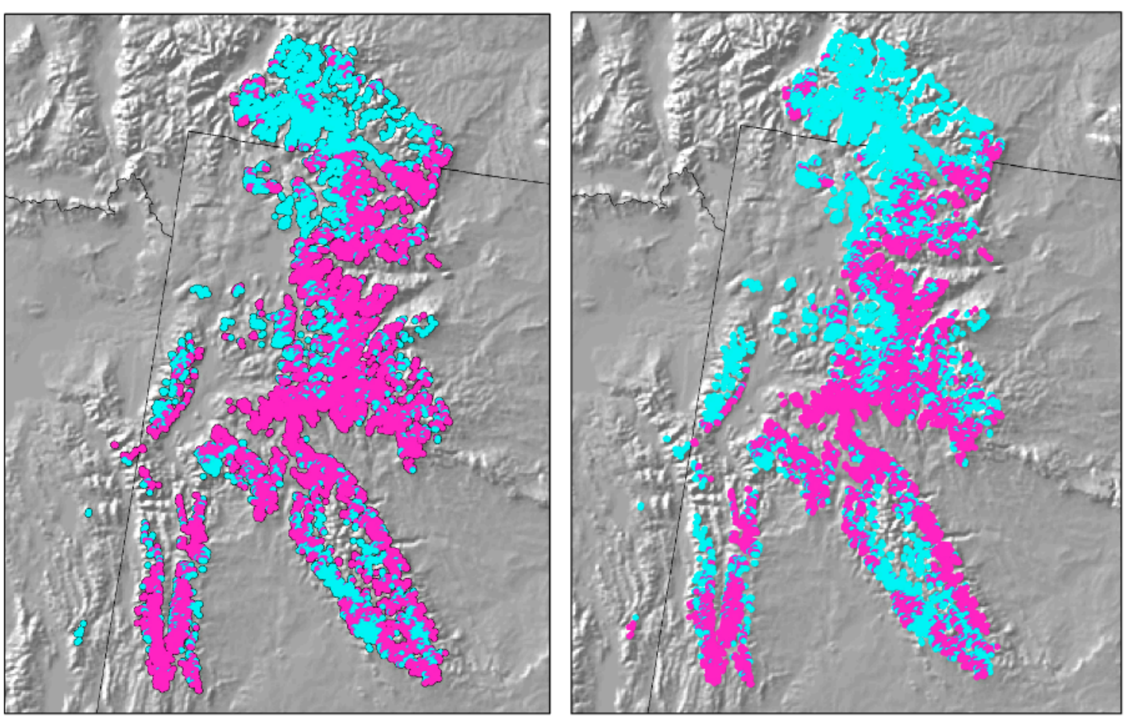

Figure 3. Areas in the Greater Yellowstone Ecosystem of whitebark mortality caused by mountain pine beetles (in pink) and without mortality (in blue) between 1998-2009 from observation (left) and model predictions (right). Predictions classified using the prevalence of pixels with mortality in 2008 (ratio of no mortality area to mortality area; 0.36).

In all three regions, adaptive seasonality was best represented by two variables; average fall and spring-summer temperature. Increasing fall temperature led to a greater probability of tree mortality. However, the influence of spring-summer temperature is uncertain, as indicated by the wide standard errors (Figures S4-S6).

The influence of drought stress on host trees was best represented by summer precipitation. In the Greater Yellowstone Ecosystem, we identified cumulative two-year summer precipitation as the most important variable (Figure S4), whereas in in the Northern Rockies we found that current summer precipitation was best (Figure S5) and in the Cascades cumulative summer precipitation over four years was most important (Figure S6). In all regions, the probability of mortality increased with decreasing precipitation (increasing drought stress), until the very lowest amounts of precipitation.

The number of dispersing beetles, or beetle pressure from outside the focal cell, was the most important individual variable in the models for each region (Figure 4). Drought stress was the most important weather variable, followed by fall temperature and winter minimum temperature. In all regions, fall and winter temperatures were suitable for a few years before the outbreak, and drought conditions occurred during the first year of the outbreak (Figure S7). The contribution of individual weather variables was not constant each year, but instead oscillated from negative to positive through time.

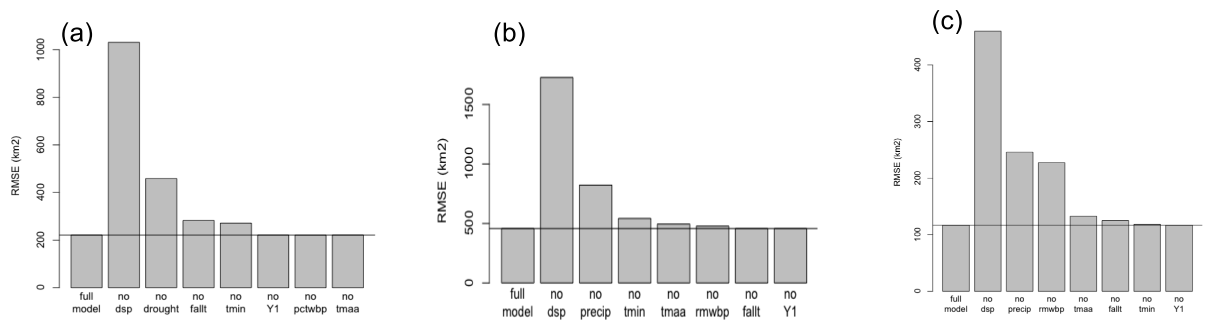

Figure 4. Variable importance in the top model of area of whitebark pine mortality from mountain pine beetles measured in terms of root mean squared error (RMSE) of mortality area each year for (a) the Greater Yellowstone Ecosystem, (b) the Northern Rockies, and (c) the Cascades. RMSE calculated by holding one variable at a time constant (e.g. “no dsp” model has constant values for the dispersal variable), with all other variables at their 1985-2009 values. See Table 1 for variable definitions.

6.2 Climate influences on the number of whitebark pines killed by mountain pine beetle

Models of outbreak severity (number of whitebark pines killed) performed well compared with observations but were less successful than those of outbreak probability. Our top models of outbreak severity captured the temporal patterns of the number of trees killed in the Greater Yellowstone Ecosystem and the Northern Rockies, but were less successful in the Cascades (Figure 5). The ecological interpretation of the unconditional outbreak severity model, including the explanatory variables selected to best represent each process and the relationships of those variables to the number of trees killed (Figures S8-S10), was similar to the probability of mortality model.

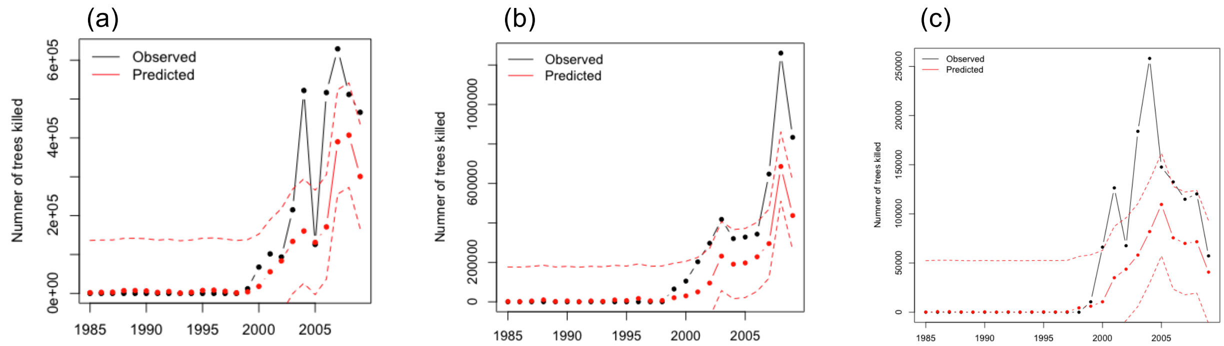

Figure 5. Observed and predicted number of whitebark pines killed from mountain pine beetles in (a) the Greater Yellowstone Ecosystem from 1985 through 2009, R^2 = 0.85; (b) the Northern Rockies, R^2 = 0.98; and (c) the Cascades, R^2 = 0.85.

6.3 Historical weather suitability

Historical weather suitability patterns were similar for the probability of mortality and outbreak severity models; results are shown for the top mortality probability model for each region (Figure 6). The most noticeable feature in these patterns is the number of consecutive years with a lack of low suitability during the 1998-2009 outbreak period. In addition to the overall climate suitability, we considered the influence of each climate variable separately (Figure S11). Individual weather variable suitability fluctuated during the last 110 years; however, winter minimum temperature and average fall temperature remained suitable during the recent outbreaks (since 2000) in all regions. In contrast, earlier decades in each region have climate conditions that are less favorable for beetle outbreaks. Warming winters appear to be the primary reason for this change to more suitable weather conditions for mountain pine beetle outbreaks. Drought conditions favorable for beetle outbreaks occurred throughout the last 110 years, with a high degree of interannual variability. These patterns are similar across each region, although the negative influence of winter temperature appears much stronger in the Northern Rockies than in the other two regions.

6.4 Climate change sensitivity

Sensitivity of outbreak area and severity to changes in a climate variable (with other climate and non-climate variables held at their observed values) varied depending on the climate variable. In the Greater Yellowstone Ecosystem, outbreak probability and severity was sensitive to increases in winter maximum temperature, with increases of 15-20% associated with warming of 3-5 ºC (Figure S12), and to changes in summer precipitation that resulted in +10 to -35% changes in outbreak area and severity. In the Northern Rockies, outbreak probability and severity were most sensitive to increases in fall temperature, with 60-100% increases from increases by 5 ºC (Figure S13). Changes in precipitation exhibited similar but weaker patterns to those in the Greater Yellowstone Ecosystem. In the Cascades, large increases occurred with small temperature increases in fall and winter (0.5 ºC), and, because of clamping, additional warming had little or no additional effect on outbreaks (Figure S14). Changes in precipitation were similar to those from the Greater Yellowstone Ecosystem. Among regions, increasing temperatures generally led to more outbreak area and higher severity, although in the Northern Rockies, higher winter temperatures led to decreased outbreak area and severity. Outbreak area and severity increased with decreasing precipitation, with the largest effect with only a small decrease. Increasing precipitation led to decreased outbreak area and severity.

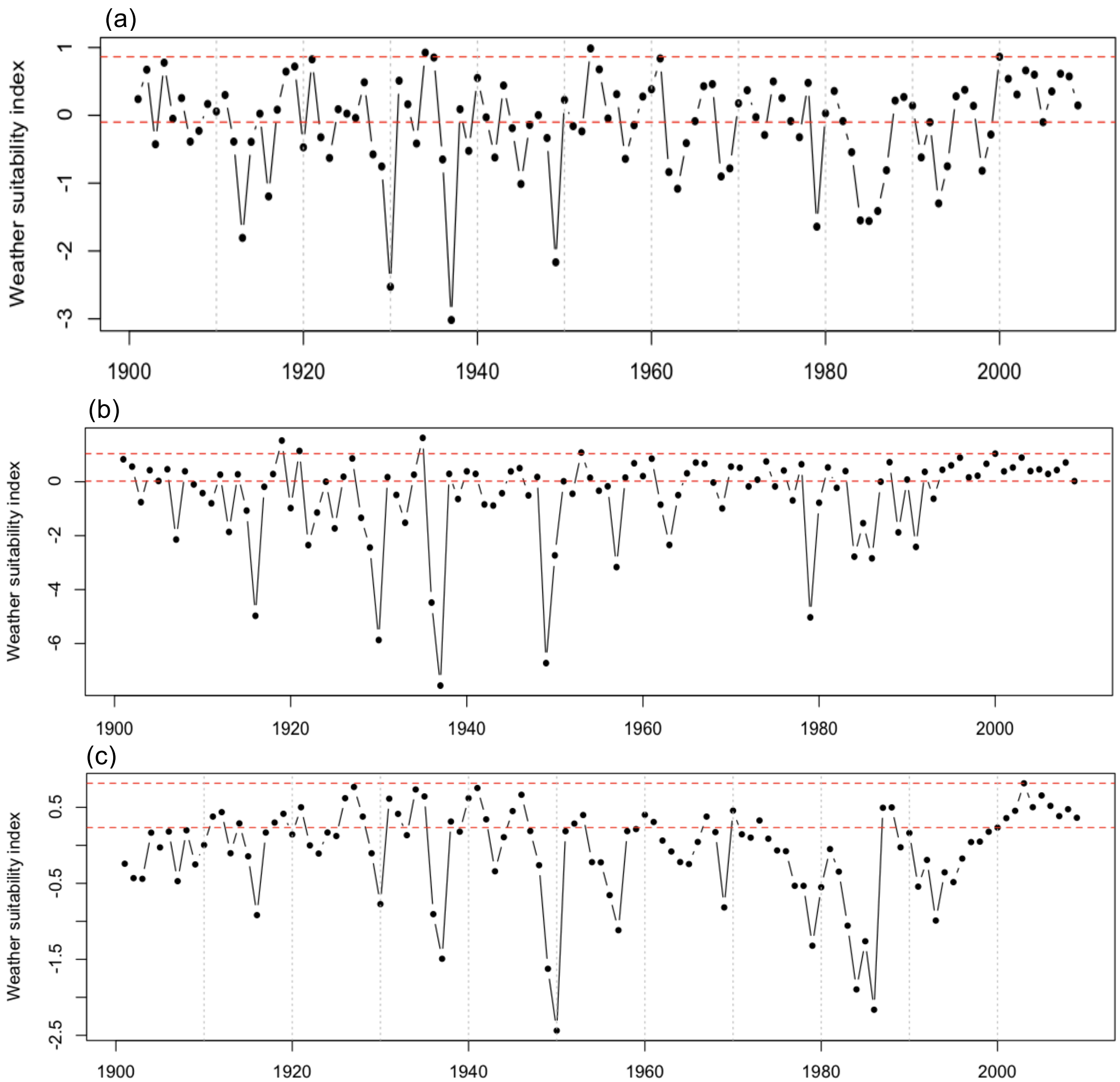

Figure 6. Spatially averaged historic weather suitability calculated from the top model of the probability of mortality due to mountain pine beetles for the (a) Greater Yellowstone Ecosystem, (b) the Northern Rockies, and (c) the Cascades from 1900-2009. Dashed red lines bound weather suitability during the 1998-2009 outbreaks.

6.5 Change in outbreak resulting from future climate change

We assessed the impact of future climate change for the Greater Yellowstone Ecosystem region; analyses of the other regions are forthcoming and will be included in subsequent presentations and publications. We quantified changes in climate variables identified above as important for mountain pine beetle outbreaks from climate model projections (Figures S14-S16). All projections had reduced summer precipitation in the coming decades compared with recent periods, and therefore our GCM selection process was unsuccessful in identifying a wetter climate model. We hypothesize three reasons for this. First, our GCM selection process was based on averages from the entire West, not just the Greater Yellowstone Ecosystem. However, inspection of maps suggests that the Greater Yellowstone Ecosystem may be at least average in terms of precipitation compared with the West, and in some cases is wetter than other regions. Second, our selection process was based on future changes relative to model estimates of historical conditions, yet we show comparisons with actual observations (to better connect with observed beetle outbreaks). It is possible that the model estimates for the historical time period are substantially drier than the observations, such that projected increases in the model estimates remain below observed precipitation. Third, our model selection process was based on comparisons of the original resolution GCM results. Conversations with John Abatozglou (UI), Katherine Hegewisch (UI), and David Rupp (OSU) revealed that the downscaling process may alter the magnitude and sign of precipitation changes relative to the coarse-resolution changes. We plan to refine our model selection process to identify a wet model for use in projections.

Our preliminary results suggest similar patterns for mortality area and outbreak severity, and we therefore present and discuss results related to mortality area only. Projections of changes in weather suitability for mortality associated with changes in climate varied among the GCMs, RCPs, and future decades (Figure 7). Changes in weather suitability resulted from the nonlinear relationships with climate variables, including the positive or neutral relationships with temperature and negative relationship with precipitation; the relative importance of each climate variable within the models; and the variability in magnitude of warming and change in precipitation (negative, neutral, or positive). In particular, the strong influence of summer precipitation coupled with the variability in precipitation projections among models caused weather suitability projections to increase or decrease.

Median estimates of weather suitability were higher than the weather suitability in the no-outbreak period (1986-1995), and substantial increases were estimated for some projections. Compared with the years of current outbreak (2000s), projection results were lower, similar, or higher (i.e., substantial variability occurred).

The climate influence on outbreaks at higher levels of warming associated with more emissions, later decades, or warmer GCMs was limited by our use of clamping to avoid extrapolation of climate/beetle relationships beyond observed values of temperature and precipitation. With some processes, clamping may be a reasonable approach. For instance, warmer winters above some threshold are unlikely to result in reduced beetle mortality, and more precipitation in very wet summers may not increase suitability for outbreaks. In the Greater Yellowstone Ecosystem, temperature/outbreak area relationships plateaued at high temperatures, limiting the effect of clamping.

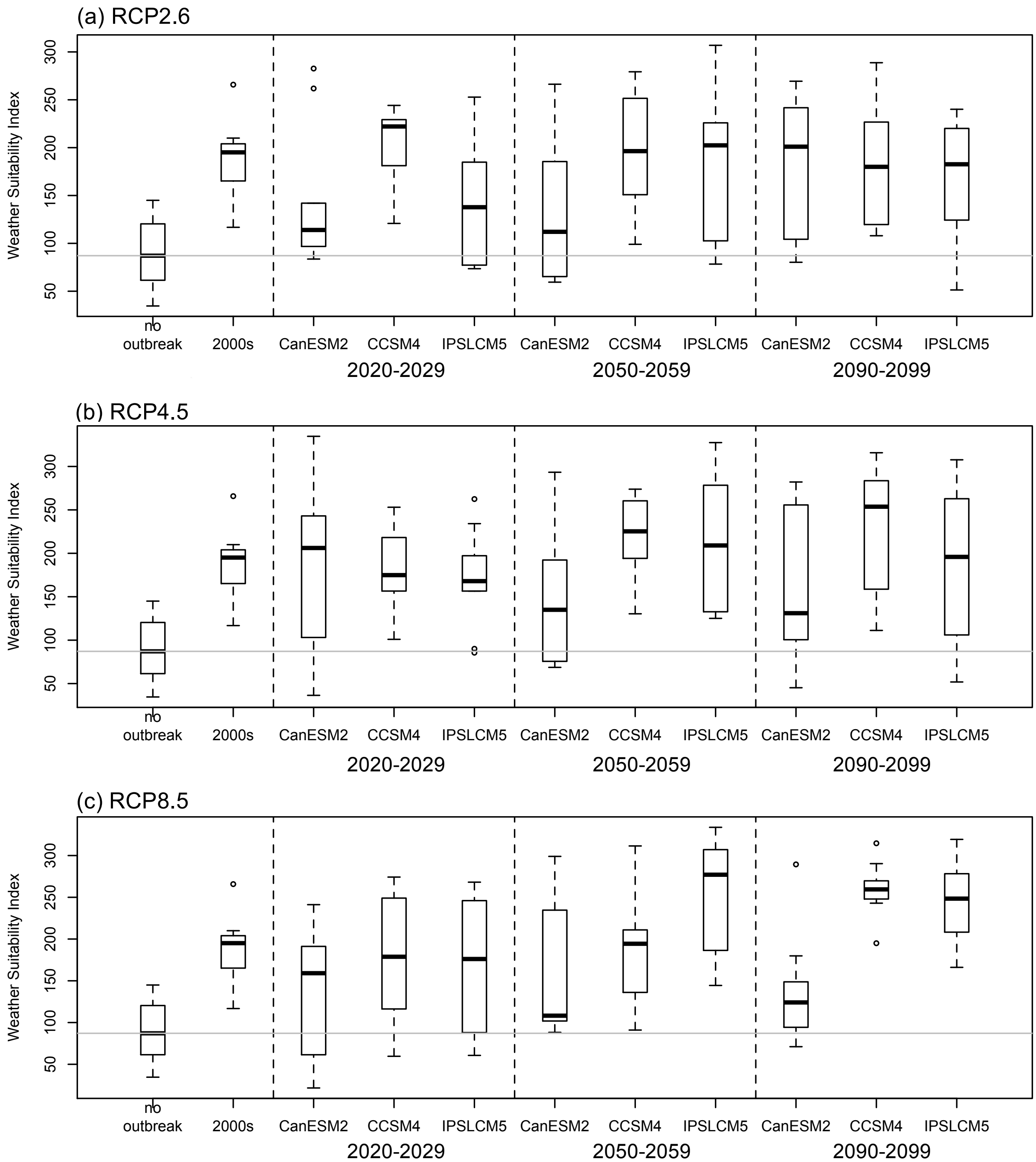

Figure 7. Preliminary results showing modeled weather suitability index for the area of whitebark pine mortality from mountain pine beetles within the Greater Yellowstone Ecosystem, including the period without outbreaks during 1985-1994, the current outbreak period (2000-2009), and future decades using climate change projections. Future suitability estimated using three general circulation models (GCMs; CanESM2 (warmer and wetter), CCSM4 (reduced warming, little change in precipitation), and IPSL-CM5A-MR (warmer and drier)) and for three representative concentration pathways: (a) RCP2.6, (b) RCP4.5, and (c) RCP8.5. Box plots show distributions of annual values during periods (N=10). Horizontal gray line shows median weather suitability index during the 1986-1995 period. Please check with authors for updates before using this figure.

7. ANALYSIS AND FINDINGS

Our study added to the body of scientific knowledge on climate influences on bark beetle outbreaks in three main ways. First, our study is the first to evaluate the full suite of climate influences on mountain pine beetle outbreaks in whitebark pine. Differences between whitebark pine susceptibility and that of another major and better-studied host, lodgepole pine, have been document in stand-scale studies (Raffa et al. 2013). Ours is the first to quantify climate/beetle relationships in whitebark pine forests. We found higher probability of mortality area and number of whitebark pines killed with warmer and drier conditions. The increase in mortality probability and severity associated with increased temperatures agrees well with current understanding of mountain pine beetle population dynamics. Higher fall temperature allows for the continued development of eggs laid late in the fall so the majority of the cohort enters the winter in the most cold-hardy developmental stage, and synchronizes the population so that there is a mass emergence of adults the following summer (Logan and Powell 2001). Higher winter minimum temperature reduces the chances of beetle mortality during cold seasons (Logan and Powell 2001, Régnière and Bentz 2007). Our modeling suggests a positive but inconclusive influence of spring-summer temperature on mortality probability and outbreak severity. An alternate explanation may be that the range of spring-summer temperature variability over the period of model development may have been insufficient to detect an influence. Jewett et al. (2011) similarly found that whitebark pine mortality in the Greater Yellowstone Ecosystem was related to warmer conditions.

Drought influences the susceptibility of lodgepole pine to mountain pine beetle attack (Raffa and Berryman 1983). However, the effect of drought is less well established in whitebark pine (Logan et al. 2010), though Millar et al. (2012) found drought in the previous one to two years was associated with whitebark pine mortality in the Sierra Nevada. Our results indicate a strong influence of summer drought on both outbreak probability and severity. There is some correlation between drought and temperature, and it is possible the drought effect we found is a combination of host tree stress and beetle development effects. However, precipitation best represented drought and was also the least correlated with temperature (compared with climatic water deficit and vapor pressure deficit), suggesting that the influence of this variable is on host tree stress. We suggest that further work is necessary to fully understand the role of drought in this system.

Beetle pressure had an increasingly important influence on mortality probability and outbreak severity as the outbreak progressed. At low beetle pressure, dispersal from neighboring cells was more strongly limiting mortality probability and outbreak severity than were beetles originating from trees killed within the cell of interest (focal cell). This finding suggests that early in the outbreak, beetle populations were increasing in nearby, potentially more hospitable, habitats and dispersing to whitebark pine forests. As the outbreak progressed and weather conditions continued to be suitable, the influence of beetle pressure from the focal cell increased, but never equaled the influence of dispersal. The decline in mortality probability and outbreak severity at the highest beetle pressure within focal cell is likely due to a lack of suitable living host trees. To account for host tree availability, we included remaining whitebark pine as an explanatory variable in the Northern Rockies and Cascades regions. As remaining whitebark declined, so did the probability of mortality and outbreak severity. In the Greater Yellowstone

Ecosystem, this variable was strongly positively correlated with percent whitebark pine and was not included in the final models because doing so resulted in a poorer model.

The relationships that we found between mountain pine beetle outbreak characteristics and climate, stand structure, and beetle pressure in whitebark pine forests were similar to previous empirical studies in lodgepole pine (Carroll et al. 2004, Aukema et al. 2008, Preisler et al. 2010, Sambaraju et al. 2012).

The second major finding is associated with the climate influences on the current outbreaks of mountain pine beetle in whitebark pine forests. These recent outbreaks across the western United States appear to have been initiated by several years of favorable winter minimum and fall average temperatures combined with drought conditions. Temperatures remained suitable throughout the period of outbreaks, but drought conditions fluctuated during the course of the outbreaks.

Weather suitability fluctuated from 1900 through 2009. The current outbreaks occurred during a period without very low suitability for a number of years in a row. Combined with the observed variation in temperature variables from 1900 through 2009, this suggests that years with extremely low temperatures, particularly in fall and winter, have previously exerted a strong influence in limiting mountain pine beetle outbreaks, but that recently, this limitation no longer occurs. This interpretation follows from mathematical descriptions of life-stage specific temperature thresholds in beetle development (Logan and Powell 2001, Powell and Logan 2005, Logan and Powell 2009) as well as the importance of low cold season temperatures causing beetle mortality (Wygant 1940, Régnière and Bentz 2007).

The third major finding is related to continued or increased favorability of climate conditions for outbreaks in whitebark pine forests. Based on our analyses, mortality area and outbreak severity will increase in response to future increases in fall and winter temperature. Slight reductions in precipitation (increased host tree stress) will result in large increases in outbreaks, and increases in precipitation will reduce outbreak potential. If the occurrence of extremely cold winters has prevented outbreaks in the past, as suggested by our analysis of 1900-2009 weather, then as winter temperature increases there will be fewer years that are cold enough to limit mountain pine beetle population growth. In another modeling study, Logan et al. (2010) predicted a similar increase in mountain pine beetle survival given increasing minimum temperatures. The large effects of future changes in summer precipitation on outbreak potential should be viewed with caution, as we suggest more research is needed to fully understand this relationship in whitebark pine forests. Furthermore, projections of changes in precipitation have relatively low confidence compared with projections of warming. Our preliminary estimates of climate suitability in the Greater Yellowstone Ecosystem suggest climate conditions that are more favorable to beetle outbreaks than occurred in 1985-1994, a period of low beetle activity. Some projections for the region result in conditions comparable to or more favorable than climate during the recent outbreak, which was usual in extent and severity (Logan et al. 2010), indicating the potential for future outbreaks that are severe and extensive.

Our models did not capture the effects of stand structure, which is known to have an influence on mountain pine beetle outbreaks (Amman and Baker 1972, Shore and Safranyik 1992). Biomass and basal area were the only explanatory variables available spatially across the study area and neither was an adequate representation of stand structure (i.e., was not a explanatory variable in our top models because standard errors bounded zero along the observed range). Variables describing tree size class distribution, canopy cover, and forest composition would likely improve the models, although such data are not currently available for our study regions. The current outbreaks have altered forest structure by reducing the number of suitable host trees (Gibson 2006), which will influence the future potential for mountain pine beetle outbreaks.

8. CONCLUSIONS AND RECOMMENDATIONS

8.1 Conclusions and recommendations

We found that climate is an important factor influencing mountain pine beetle outbreaks in whitebark pine forests. Both the direct effects of temperature on beetles through fall and winter temperatures as well as the indirect effects of summer drought on host trees influenced mortality area and severity (number of trees killed). Among regions, we identified generally similar important climate variables and similar relationships to beetle outbreak and severity. Beetle outbreaks in recent years in the Greater Yellowstone Ecosystem, the Northern US Rocky Mountains, and the Cascade Range were facilitated by long-term winter warming that led to reduced beetle mortality during particularly cold conditions. In addition, drought conditions in the early 2000s stressed whitebark pines, making them more susceptible to attack by beetles.

Sensitivity analyses revealed that mortality area and outbreak severity changed substantially in response to changes in climate variables consistent with climate model projections for the coming decades. Warming led to substantial increases in outbreak. Slight reductions in summer precipitation (drought) resulted in more outbreak area and higher severity, whereas increases in summer precipitation led to reduced outbreaks via reduced host tree stress.

In the Greater Yellowstone Ecosystem, we applied our model using climate change projections from several GCMs and emissions scenarios for three future decades. Our preliminary results suggest increases in outbreak area and severity over the 1985-1994 period when there were no outbreaks in the region, with the magnitude of increase varying among projections. Some projections of climate suitability for outbreaks were also higher than those during the recent outbreak. Given the extensive area and severity of the current outbreak, which is highly unusual, our preliminary results suggest continued or enhanced potential for large outbreaks of mountain pine beetle in whitebark pine forests.

Based on our findings, we recommend that land managers and decision makers consider the impacts of expected climate change on mountain pine beetle outbreaks in whitebark pine when planning conservation actions. As discussed below, we lacked sufficient stand structure information to include this important variable in our analysis. However, our results confirm and extend previous studies highlighting the importance of climate in this beetle/host system.

8.2 Near-term next steps

We will accomplish the following items in the next 1-3 months. This project in whitebark pine forms the basis for another project that will apply similar methods to lodgepole pine forests and that is funded by the USDA. Therefore, we are using USDA support to finish the tasks here (because they directly address our USDA objectives).

- complete development and analysis of GCM projections in Greater Yellowstone Ecosystem, including evaluating the usefulness of mortality area and severity in addition to weather suitability (in consultation with advisory committee)

- apply GCM projections in Northern Rockies, Cascades
- seek feedback about publication and outreach from External Advisory Committee (see below), including explicit interactions with US Fish and Wildlife Service personnel working on the whitebark pine listing
- submit manuscripts to peer-reviewed scientific journals (see below)
- outreach to land managers, scientists in the form of presentations and webinars (see below)
- complete web site, one-page project description (see below)

8.3 Future directions

The lack of useful stand structure information in spatially explicit format for the western US led to our reduced capability to include stand structure, an important driver of beetle outbreaks, in our analysis. We considered several potentially good candidates, but problems emerged that we could not overcome. We attempted to use quadratic mean diameter data from the National Risk Assessment mapping program, but we found substantial inaccuracies in the georegistration of this data set. We also investigated using tree height from the National Risk Assessment, but this database reported 0s in areas of beetle kill identified from the aerial surveys, reducing our confidence in this product. We acknowledge the importance of stand structure, however, and so suggest that future research that incorporates stand structure, climate, and beetle information over large areas will be valuable to reduce uncertainties in our findings.

A co-occurring mortality agent in whitebark pine forests is white pine blister rust. The US Fish and Wildlife Service made their recommended listing of whitebark pine in part based on this invasive pathogen and its large-scale impact on whitebark pine forests. Infection levels in the Greater Yellowstone Ecosystem were estimated to be between 20-30% in 2012 (Greater Yellowstone Whitebark Pine Monitoring Working Group 2013). Bockino and Tinker (2012) suggested prior blister rust infection increased whitebark pine susceptibility to mountain pine beetle attack. Unfortunately, data on blister rust infection levels for the range of whitebark pine is not available at a 1-km^2 resolution. A model developed for a limited study area where blister rust, and stand structure, data are available would be an important contribution to the understanding of the potentially synergistic nature of the threats facing whitebark pine.

9. MANAGEMENT APPLICATIONS AND PRODUCTS

We formed an External Advisory Committee (EAC) to provide guidance and feedback on our projection. We invited members familiar with whitebark pine and mountain pine beetles across a number of different institutions (federal agencies, NGO). The table below lists our EAC:

Agency	Individual	Title	Email address
US Fish and Wildlife Service	Amy Nicholas	Biologist, Whitebark pine 12-month finding author	Amy_Nicholas@fws.gov
	Lynn Gemlo	Whitebark pine listing coordinator	Lynn_Gemlo@fws.gov
USDA Forest Service	Jesse Logan	Research Entomologist (retired)	logan.jesse@gmail.com
	Robert Keane	Research Ecologist	
	Barry Bollenbacher	Forester, Region 1	bbollenbacher@fs.fed.us
	Eric Pfeifer	Forester, Salmon-Challis National Forest	epfeifer@fs.fed.us
National Park Service	John Gross	Climate Change Ecologist, Inventory and Monitoring Division	John_Gross@nps.gov
	Dan Reinhart	Resource Management Operations Coordinator, Yellowstone National Park and Member, Whitebark Pine Subcommittee, Greater Yellowstone Coordinating Committee	Dan_Reinhart@nps.gov
	Kristin Legg	Greater Yellowstone Network Program Manager, Inventory and Monitoring Program	Kristin_Legg@nps.gov
	Roy Renkin	Vegetation Management Specialist	Roy_Renkin@nps.gov
	Tara Carolin	Formerly Park Ecologist, now Director, Research Learning Center, Glacier National Park	Tara_Carolin@nps.gov
NGOs	Louisa Willcox	Natural Resources Defense Council	lwillcox@nrdc.org

Early in the project (November 2012), we gave a webinar to the EAC describing our planned research in detail and soliciting feedback, which we then incorporated into the project. We also requested feedback via email from the EAC on specific questions about how to present our findings and what to consider for future climate projections. We plan to give another webinar to the EAC in January to present our findings and request assistance with distributing our results.

The US Fish and Wildlife Service is reviewing the listing status of whitebark pine in Spring 2014, and we will provide the listing coordinators with our publications to include in their decision.

We met with the Whitebark Pine Subcommittee of the Greater Yellowstone Coordinating Committee to discuss our preliminary results and request feedback. We have plans to continue to interact with this group as we complete our publications.

10. OUTREACH

10.1 Scientific publications

We list here the anticipated publications in scientific journals (authors, titles, journals, expected submission dates).

Buotte, P. C., J. A. Hicke, H. K. Preisler, and K. F. Raffa, “Modeling climate/mountain pine beetle relationships in whitebark pine forests in the western United States,” to be submitted to *Ecology*, February 2014.

Buotte, P. C., J. A. Hicke, H. K. Preisler, and K. F. Raffa, “Estimating the impact of future climate change on mountain pine beetle outbreaks in whitebark pine forests in the western United States,” to be submitted to *Global Change Biology*, February 2014.

Buotte, P. C., J. A. Hicke, H. K. Preisler, and K. F. Raffa, “Climate change and mountain pine beetle outbreaks in whitebark pine forests in the Greater Yellowstone Ecosystem,” to be submitted to *Ecological Applications*, February 2014.

10.2 Presentations

Past

Preisler, H. K., J. A. Hicke, and P. Buotte, “A mechanistic model for landscape level tree mortality based on beetle population dynamics,” 97th Annual Meeting of the Pacific Branch of the Entomological Society, 7-10 April 2013, Lake Tahoe, NV.

Buotte, P. C., J. A. Hicke, H. K. Preisler, and K. F. Raffa, “Understanding the influence of climate on mountain pine beetle outbreaks in whitebark pine forests,” 4th Pacific Northwest Climate Science Conference, 5-6 September 2013, Portland, OR.

Buotte, P. C., J. A. Hicke, H. K. Preisler, and K. F. Raffa, “Understanding the influence of climate on mountain pine beetle outbreaks in whitebark pine forests,” Forest Insect Disturbance in a Warming Environment, Joint Meeting of IUFRO Sections 07.03.05 and 07.03.07, 16-19 September 2013, Banff, Canada.

Buotte, P. C., J. A. Hicke, H. K. Preisler, and K. F. Raffa, “Understanding the influence of climate on mountain pine beetle outbreaks in whitebark pine forests of the Greater Yellowstone Ecosystem,” Presentation to the Whitebark Pine Subcommittee of the Greater Yellowstone Coordinating Committee, October 30, 2013, Bozeman, MT.

Planned

Invited seminar at the Missoula Fire Science Lab, Spring 2014.

Invited seminar at the USGS Northern Rockies Research Station, Spring 2014.

Western Forest Insect Work Conference, March 2014.

Ecological Society Annual Meeting, August 2014.

MtnClim Meeting, September 2014.

10.3 Webinars

We gave a webinar to our External Advisory Committee (see above) at the beginning of the project (November 28, 2012) to solicit feedback. We plan to give 1-2 additional webinars to present the results of our project to the EAC and to relevant scientists/managers/decision makers.

10.4 Communication to managers and decision makers

We will invite managers and decision makers to our webinar (described above). We will give presentations at the Western Forest Insect Work Conference in March 2014, which is attended by both managers and scientists. We are currently developing a web site that describes our results and provides maps and data (see attached screenshot, Appendix A). We will also develop a one-page description of our project and results written for managers and the general public for posting on web sites and distribution (see attached draft, Appendix B).

We will actively seek out managers and decision makers with whom to communicate. One of our External Advisory Committee members, Eric Pfeifer, has volunteered assist us with identifying the appropriate USFS regional foresters and silviculturists. Two USFWS personnel (Nicholas and Gemlo) associated with the ESA listing of whitebark pine are on our Extern Advisory Committee, and we will ensure that the USFWS decision process is aware of our project results through them. We will continue to interact with the Whitebark Pine Subcommittee of the Greater Yellowstone Coordinating Committee to apprise them of our findings.

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12. TABLES

Table 1. Description of explanatory variables included in generalized additive models.

Process	Rationale	Variable	Description	Reference
Climate Conditions				
winter mortality	unseasonably low temperatures and/or extreme low temperatures can cause direct mortality of overwintering insects	Tmin	Minimum monthly minimum temp in Dec.-Feb.	Preisler et al. (2012)
		Coldt	Probability of winter survival from the cold tolerance process model developed by	Regniere and Bentz (2007)
		Ecs	Presence/absence of an early cold snap, defined as 4 consecutive days with T <=-20°C between Oct. 15–Nov. 30	Sambaraju et al. (2012)
		Drop20	Number of days with >20°C drop in average temperature	Sambaraju et al. (2012)
		Min40	Number of days with min temp <=-40°C	Sambaraju et al. (2012)
adaptive seasonality	temperature conditions can promote outbreaks by allowing for a one-year life cycle and synchronous adult emergence	Logan	0/1 of whether conditions were suitable for univoltinism according to adaptive seasonality process model	Logan and Powell (2001)
		Tmean	Average temp Aug 1 – July31	Preisler et al. (2012)
		Tmaa	Average temp April-Aug	Preisler et al. (2012)
		CDD	Cumulative degree days above 5.5°C from Aug. 1–July 31; DD = max(0,T-Tthresh)	Aukema et al. (2008), Sambaraju et al. (2012)
		BDD	Binary of whether 833°C degree days accumulated between Aug 1 – July 31	Aukema et al. (2008), Sambaraju et al. (2012)
flight conditions	optimal temperatures exist for adult flight	Tma	Average monthly temperature in August	Carroll et al. (2004), Preisler et al. (2012), Aukema et al. (2008)
available food supply	available brood food supply increases with	VPD1	Average monthly vapor pressure deficit in the previous growing season	Sambaraju et al. (2012)

	increasing phloem thickness, here represented by growth conditions in the previous year	CWD1	Climatic water deficit in the previous growing season[1]	
		PPT1	Oct.-Aug. precipitation in previous year	
		JJAPPT1	June-Aug. precipitation in previous year	
drought stress	drought-stressed trees have lower defensive capabilities than healthy trees	VPD0-5	Average monthly vapor pressure deficit in current and previous 5 growing seasons[1] (six variables: 0, 0-1, 0-2, …, 0-5)	
		CWD0-5	Cumulative climatic water deficit in current and previous 5 growing seasons[1] (six variables: 0, 0-1, 0-2, …, 0-5)	
		PPT0-5	Cumulative monthly Oct-Aug precipitation in current and previous 5 years (six variables: 0, 0-1, 0-2, …, 0-5)	Preisler et al. (2012)
		JJAPPT 0-5	Cumulative monthly June-Aug precipitation in current and previous years (six variables: 0, 0-1, 0-2, …, 0-5)	Preisler et al. (2012)
Stand characteristics				
tree size and age	beetles are attracted to larger trees; older (larger) trees have lower defensive capabilities, thicker phloem	QMD	Average quadratic mean diameter	Shore and Safranyik (1992)
competition	competition from other trees reduces tree vigor and defensive capabilities	BA	Average basal area	Shore and Safranyik (1992)
		Biomass	biomass	Shore and Safranyik (1992)
available host	outbreaks will collapse when available host is depleted	Rmwbp	Remaining whitebark pine = cumulative mortality area since 1998 times % forest in 1-km grid cell time % of basal area that is whitebark pine	Meddens et al. (2012)
beetle pressure				
population last year	beetles can kill healthy trees at high	Y1	Number of beetle-killed trees in the focal cell in the previous year	Shore and Safranyik (1992), Preisler et al. (2012)

dispersal	populations	btp1	Weighted linear function of number of beetle-killed trees of any host species in surrounding 1-km cells up to 6 km distant, outside the focal cell, in the previous year	Preisler et al. (2012)

[1]growing season = March-October

Appendix A. Web site under development that describes our project and results.

Mountain pine beetle outbreaks in whitebark pine

- **Home**
- Methods
- Maps
- Download data
- Links

The Issue

Whitebark pine is a high-elevation, keystone tree species that is critical habitat for wildlife such as grizzly bears, influences soil and snow processes, and provides ecosystem services valued by the public. These trees are currently subjected to multiple threats, including attack by mountain pine beetle, an aggressive bark beetle that has recently killed whitebark pines over hundreds of thousands of acres in the western US. Climate is an important factor in outbreaks of this beetle through effects on the beetle via warming and on the host tree via stress associated with warming and drought. Future climate change is expected to increase the number, frequency, and/or severity of these epidemics.

Project objectives

Our project developed an empirical model of mountain pine beetle outbreaks in whitebark pine using observations of beetle-killed trees, climate, and stand conditions. We used this model to assess the relationships between climate and beetle outbreaks, including evaluating regional differences. We also used this model to understand the causes of recent outbreaks as well as produce projections of beetle outbreaks in whitebark pine given future scenarios of climate change.

Appendix B. One-page description of our project and results targeted toward managers and decision makers.

Climate and Mountain Pine Beetles in Whitebark Pine Forests across the Western US

Jeff Hicke[1], Polly Buotte[1], Haiganoush Preisler[2], and Ken Raffa[3]
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[2]Pacific Southwest Research Station, USDA Forest Service, Albany, CA
[3]University of Wisconsin-Madison

A project supported by the USGS Northwest Climate Science Center, with additional funding from the USGS Western Mountain Initiative and the USFS Western Wildland Environmental Threat Assessment Center

Issue

Whitebark pine is a high-elevation, important tree species that provides critical habitat for wildlife, influences ecosystem processes, and supplies valued ecosystem services. These trees are currently subjected to multiple threats, including attack by mountain pine beetle, which has recently killed whitebark pines over much of the western US. Climate is an important factor in outbreaks of this beetle, and future warming is expected to affect epidemics.

Objectives

Our project developed statistical models of mountain pine beetle outbreaks in whitebark pine using observations of beetle-killed trees, climate, and stand conditions for three regions: the Greater Yellowstone Ecosystem, the Northern US Rockies, and the Cascade Mountains. We assessed relationships between climate and beetle outbreaks, evaluated the climate influences on recent outbreaks, and projected future beetle outbreaks given future scenarios of climate change.

Findings

These models fit the observations well, increasing confidence in their reliability. We found that climate influenced mountain pine beetle outbreaks through fall and winter temperatures, which are direct effects on the beetles, as well as drought stress on host trees via reduced summer precipitation. Recent mountain pine beetle outbreaks in whitebark pine forests of the western United States were caused by warming as well as drought in the early 2000s. We estimated the effect of future climate change on beetle outbreaks in the whitebark pine forests of the Greater Yellowstone Ecosystem using a variety of climate projections. Our results suggest that, compared with a baseline of 1986-1995 in which little beetle activity occurred, future climate will be more favorable for mountain pine beetle outbreaks in whitebark pine. Some projections were similar to or exceed the climate favorability of conditions during the recent severe and extensive outbreak (2000-2009). Variability exists among projections as a result of the amount of future warming and changes in precipitation, which are functions of climate model, emissions scenario, and decade.

Conclusions

Our results provide quantitative evidence of the importance of climate for influencing recent and future beetle outbreaks in whitebark pine forests, and lead to increased understanding of threats to whitebark pine. We recommend that land managers and decision makers consider the impacts of expected climate change on mountain pine beetle outbreaks in whitebark pine susceptible when planning conservation actions.

Contact: *Jeff Hicke, University of Idaho, 208-885-6240, jhicke@uidaho.edu*

Appendix C. Supplementary figures.

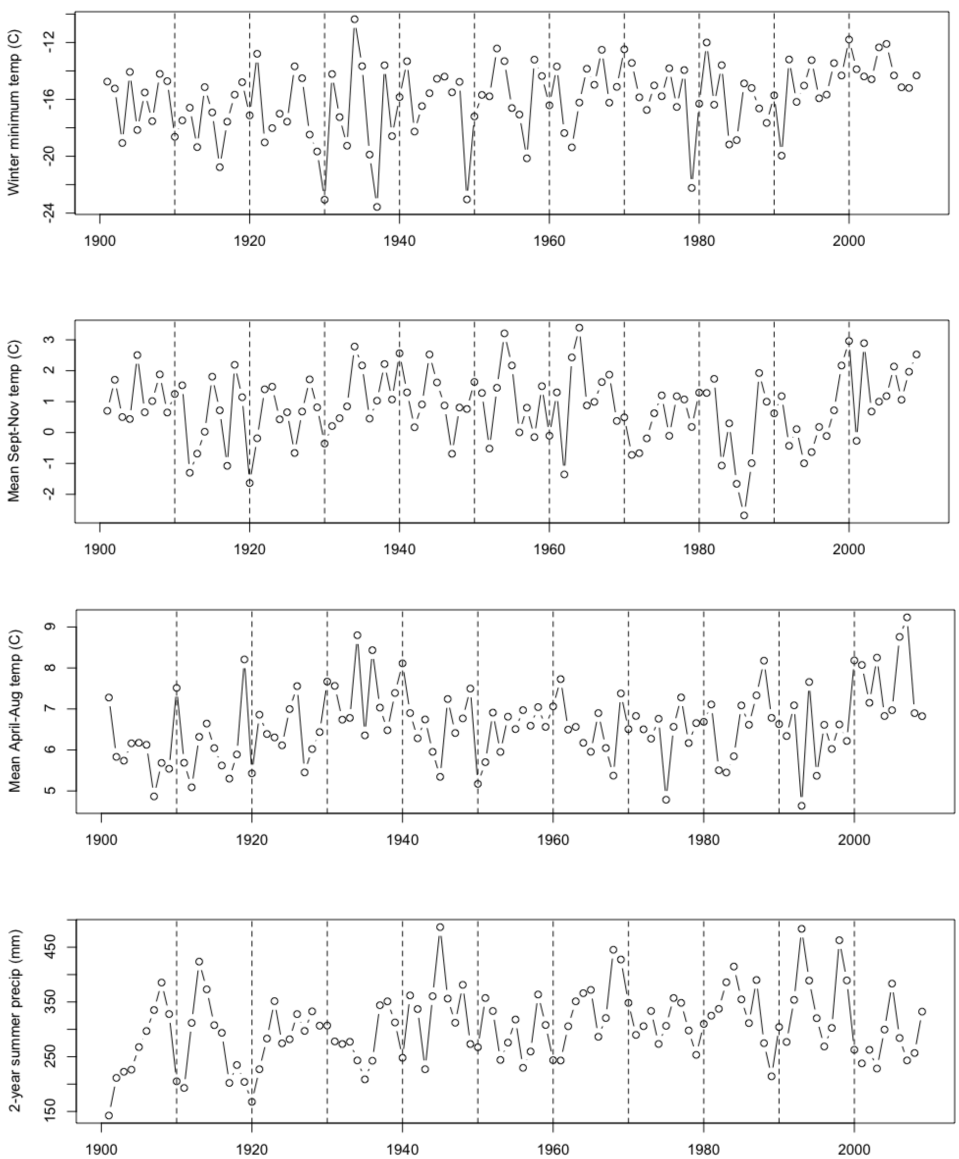


Figure S1. Weather variables averaged spatially across the Greater Yellowstone Ecosystem from 1900-2009.

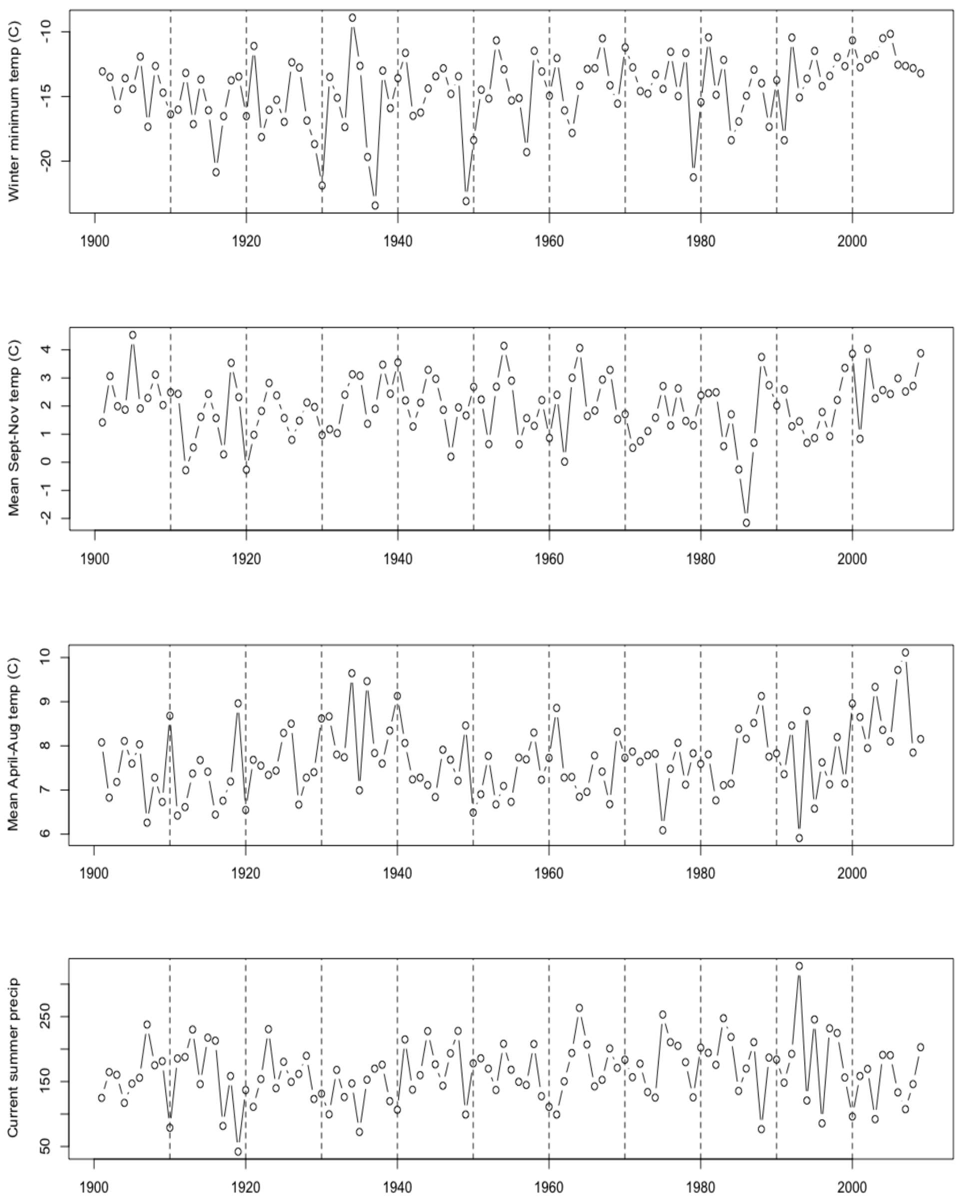


Figure S2. Weather variables spatially averaged across the Northern Rockies from 1900-2009.

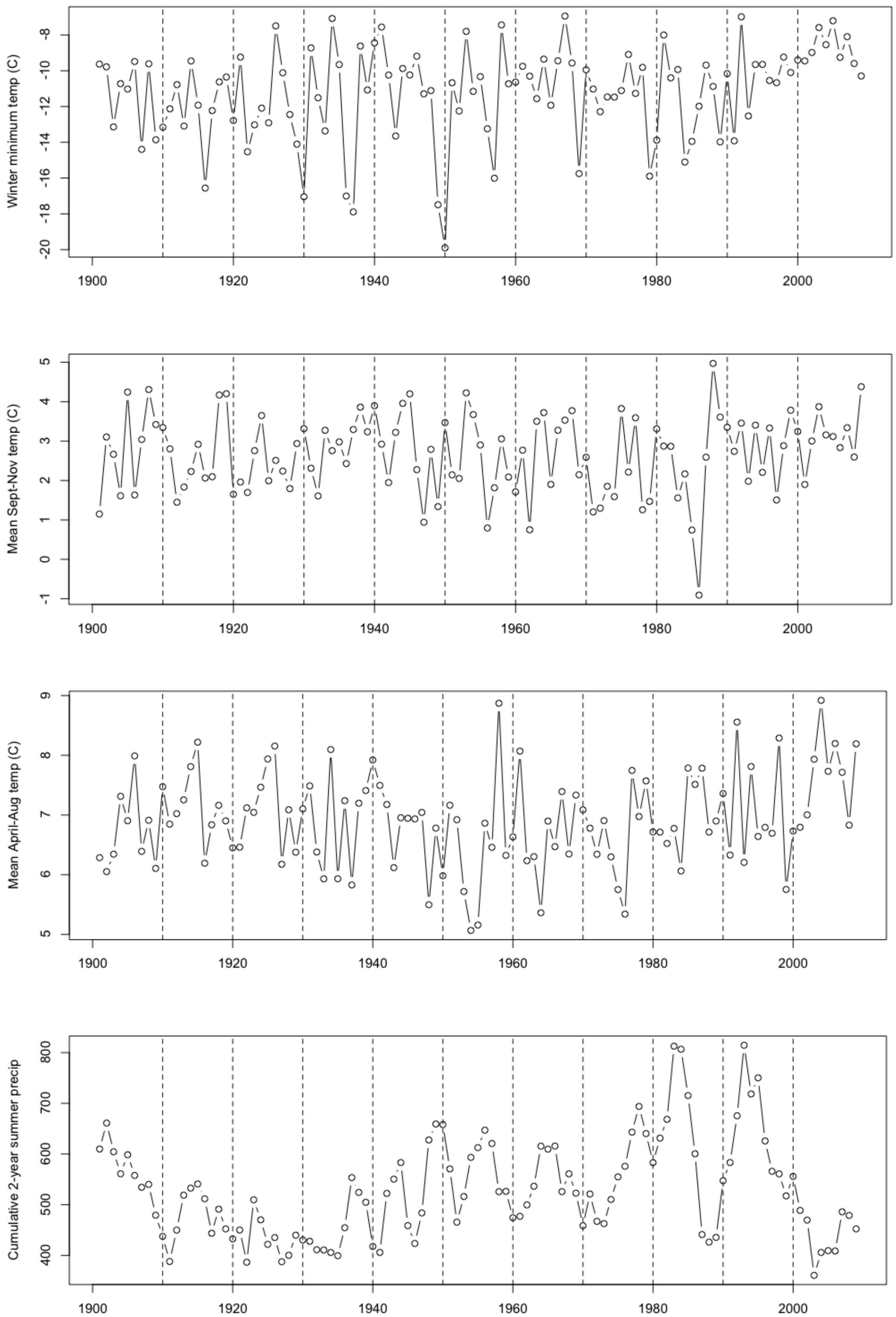


Figure S3. Weather variables spatially averaged across the Cascades from 1900-2009.

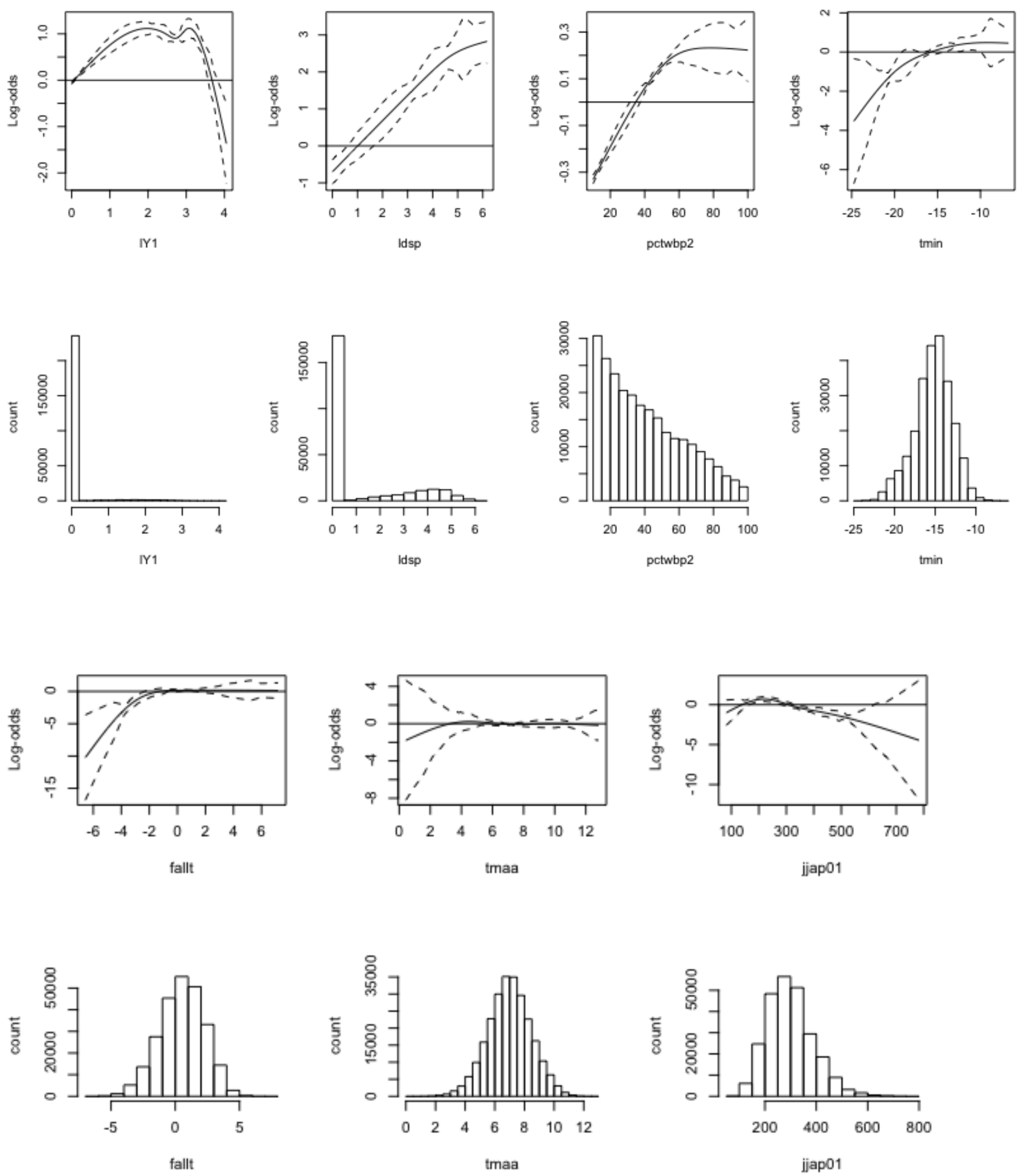


Figure S4. Log-odds plots showing relationships of explanatory variables to area of whitebark pine mortality from mountain pine beetles in the Greater Yellowstone Ecosystem, and histograms of values within study area and period. Dashed lines indicate standard errors calculated from jackknifing by year. See Table 1 for variable definitions.

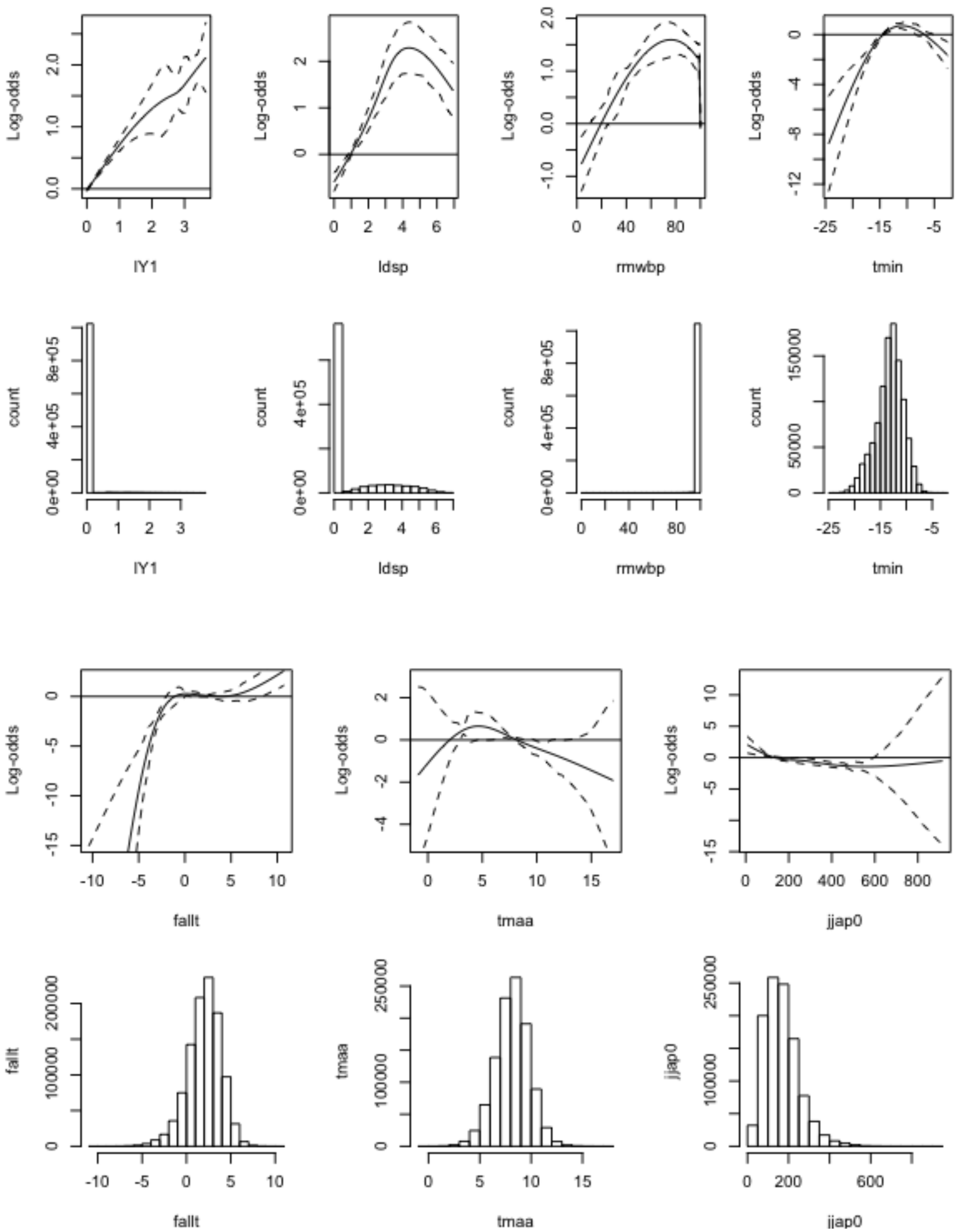


Figure S5. Log-odds plots showing relationships of explanatory variables to area of whitebark pine mortality from mountain pine beetles in the Northern Rockies, and histograms of values within study area and period. Dashed lines indicate standard errors calculated from jackknifing by year. See Table 1 for variable definitions.

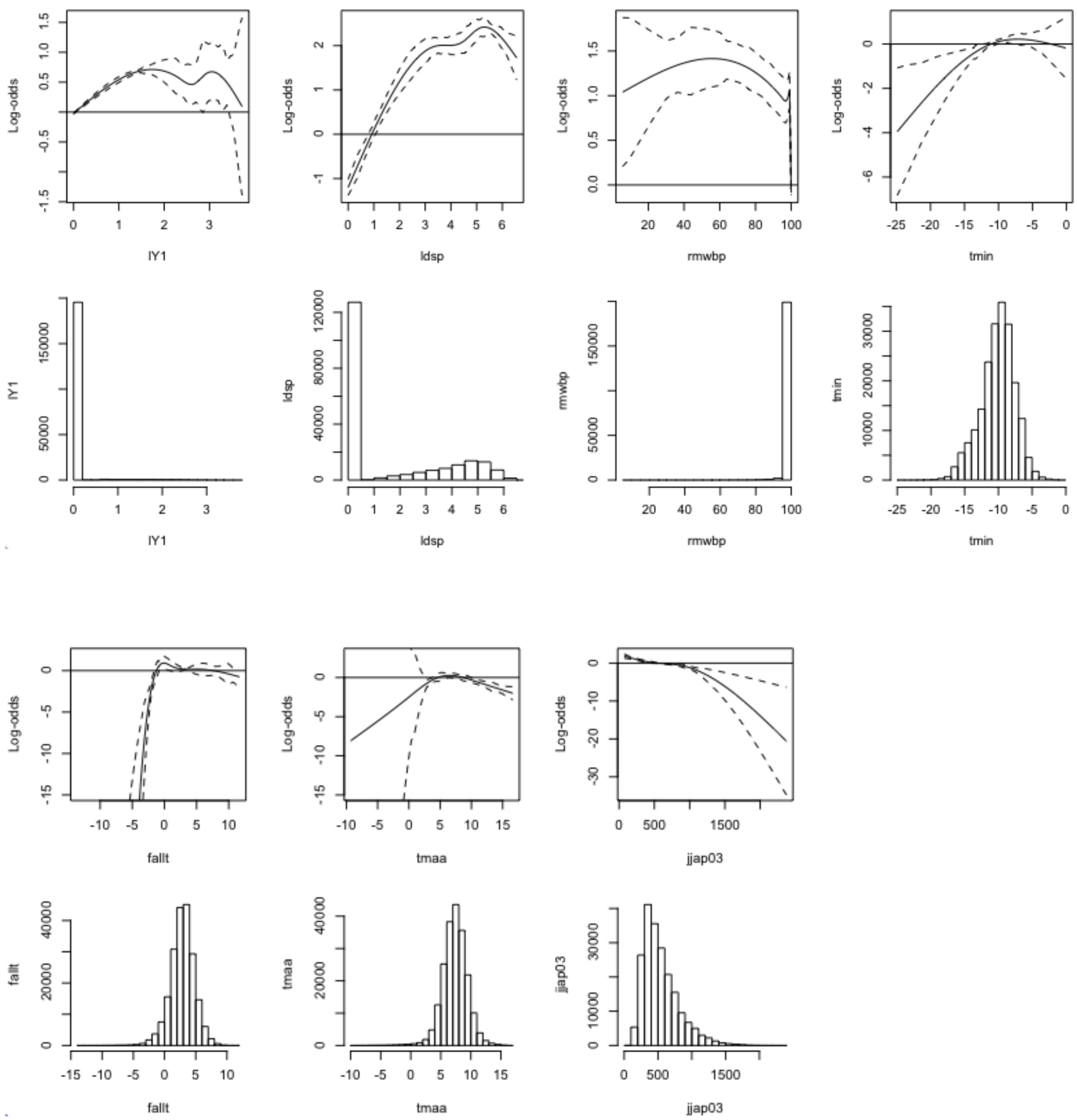
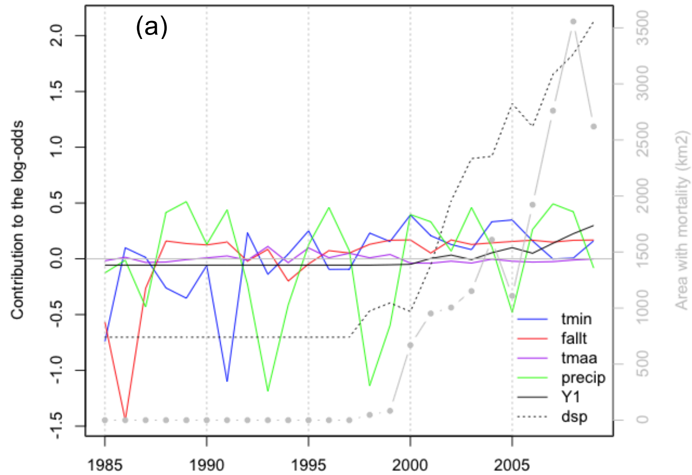
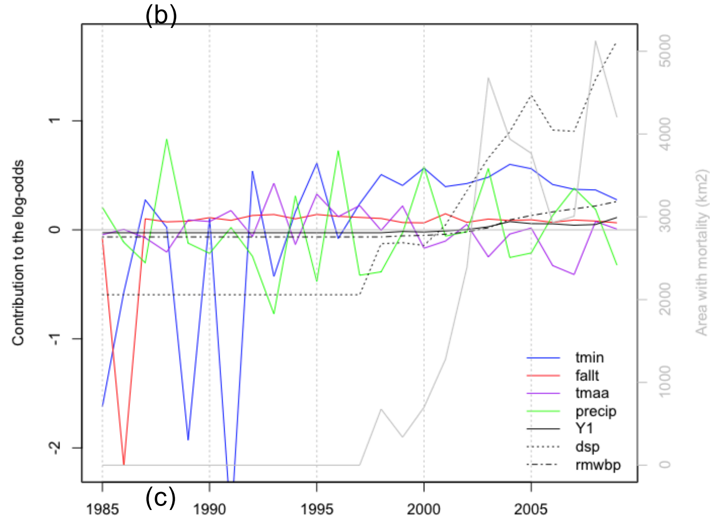


Figure S6. Log-odds plots showing relationships of explanatory variables to area of whitebark pine mortality from mountain pine beetles in the Cascades, and histograms of values within study area and period. Dashed lines indicate standard errors calculated from jackknifing by year. See Table 1 for variable definitions.





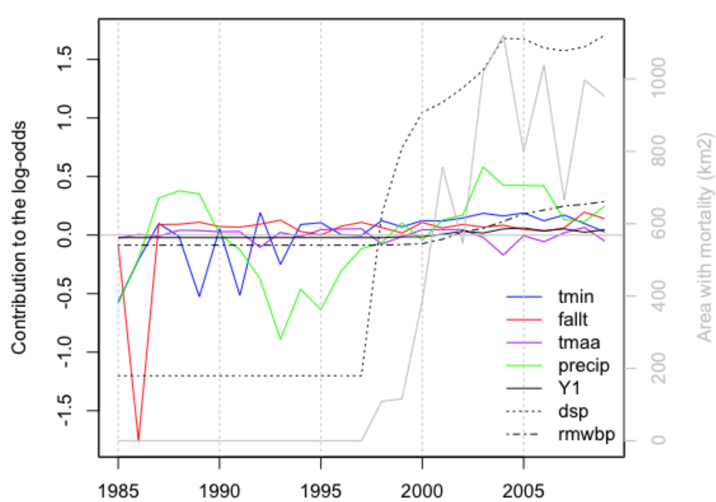


Figure S7. Spatially averaged contribution to the log-odds of mortality from mountain pine beetles for individual variables over the period of model development for (a) the Greater Yellowstone Ecosystem, (b) the Northern Rockies, and (c) the Cascades. See Table 1 for variable definitions.

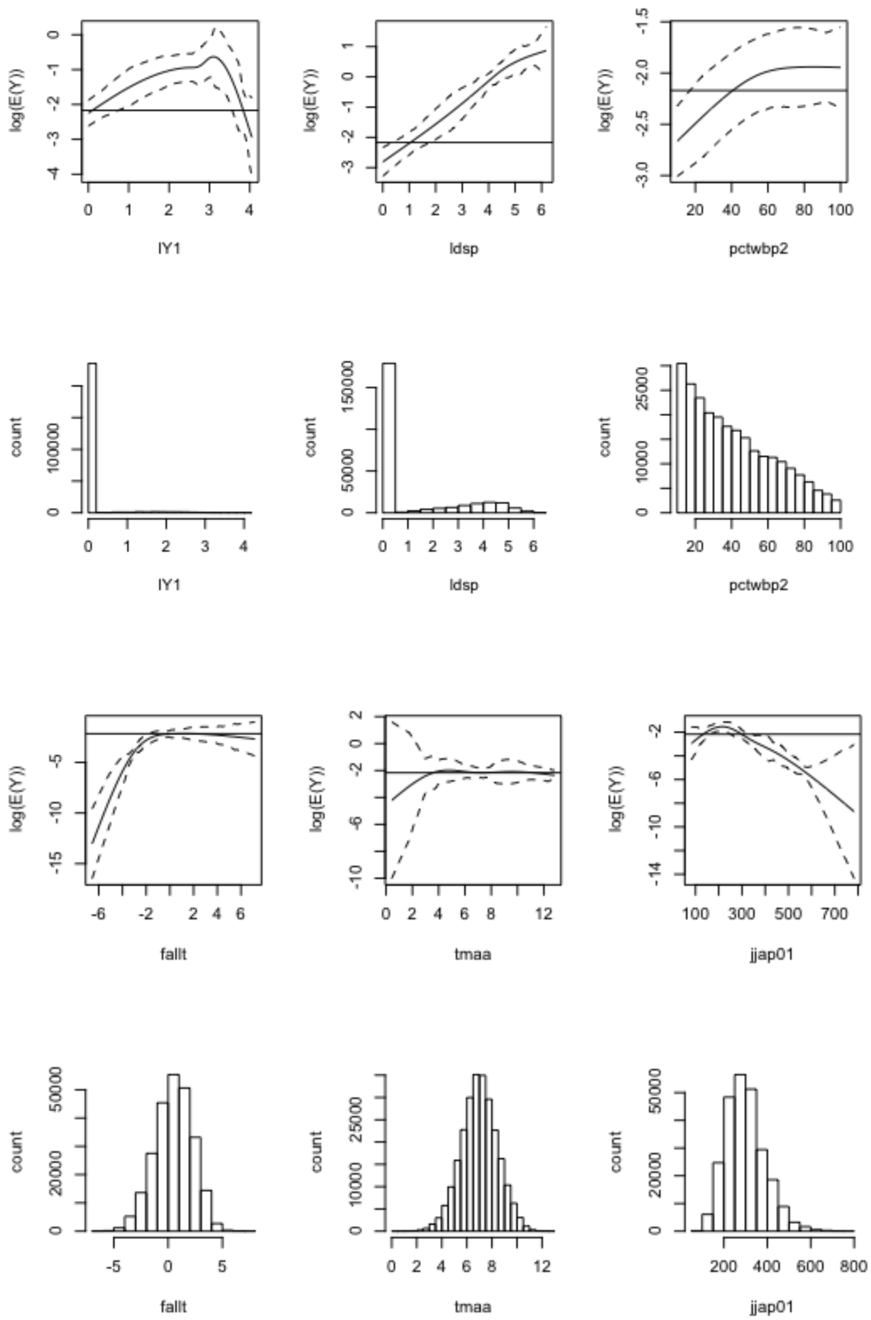


Figure S8. Response plots for the unconditional number of trees killed by mountain pine beetles in whitebark pine forests in the Greater Yellowstone Ecosystem and histograms of independent variables. Dashed lines indicate standard errors calculated from jackknifing by year. See Table 1 for variable definitions.

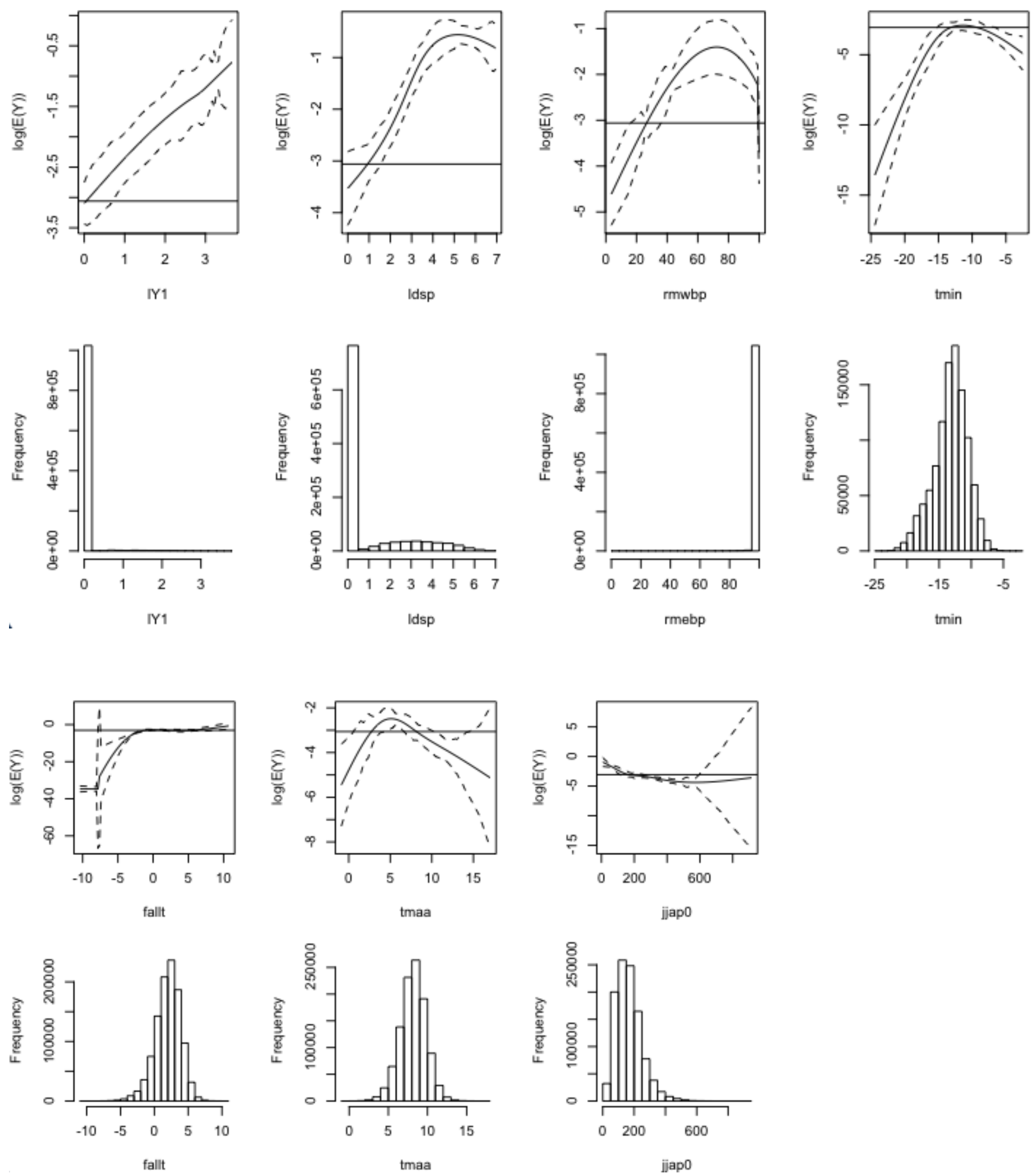


Figure S9. Response plots for the unconditional number of trees killed by mountain pine beetles in whitebark pine forests in the Northern Rockies and histograms of independent variables. Dashed lines indicate standard errors calculated from jackknifing by year. See Table 1 for variable definitions.

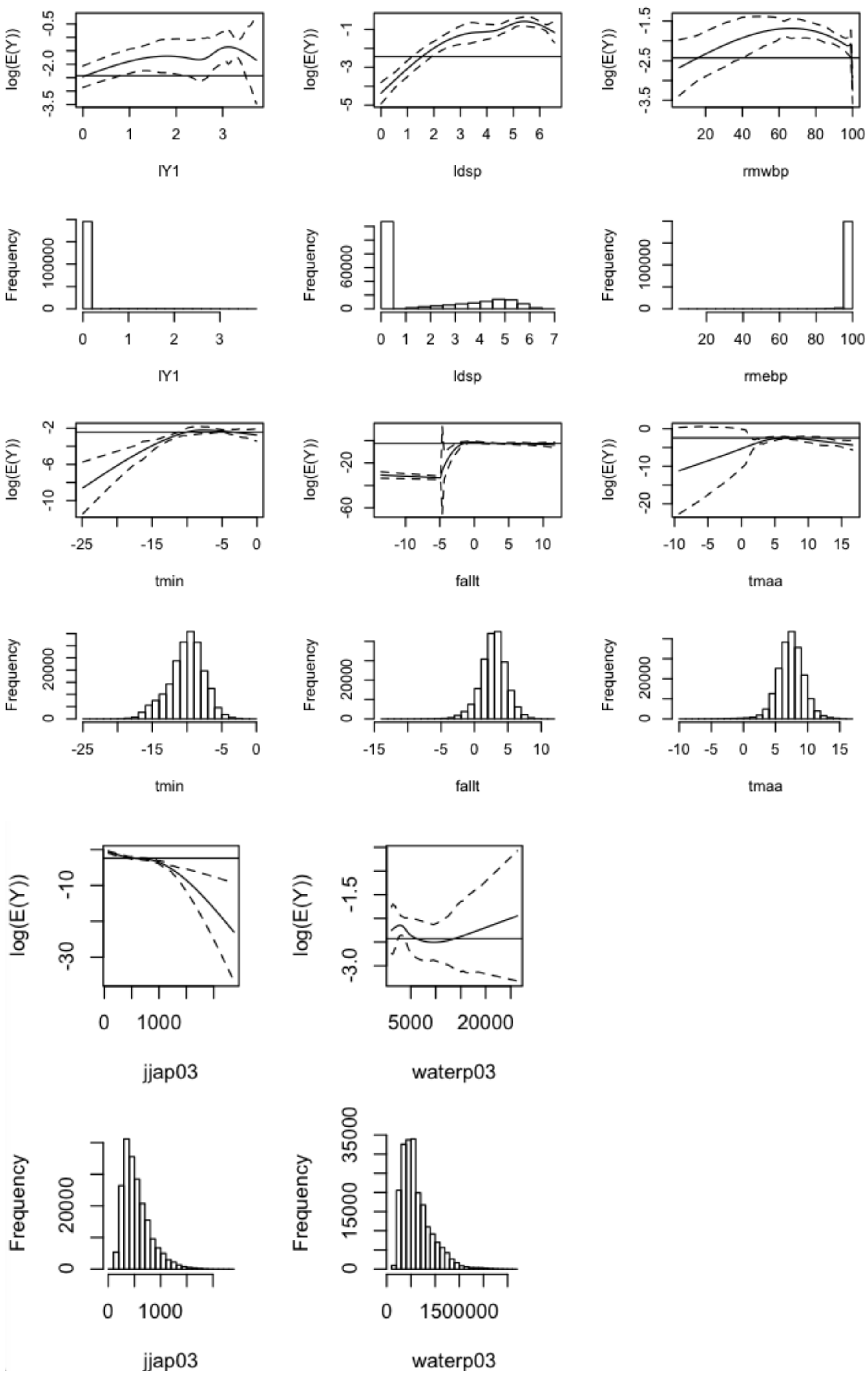


Figure S10. Response plots for the unconditional number of trees killed by mountain pine beetles in whitebark pine forests in the Cascades and histograms of independent variables. Dashed lines indicate standard errors calculated from jackknifing by year. See Table 1 for variable definitions.

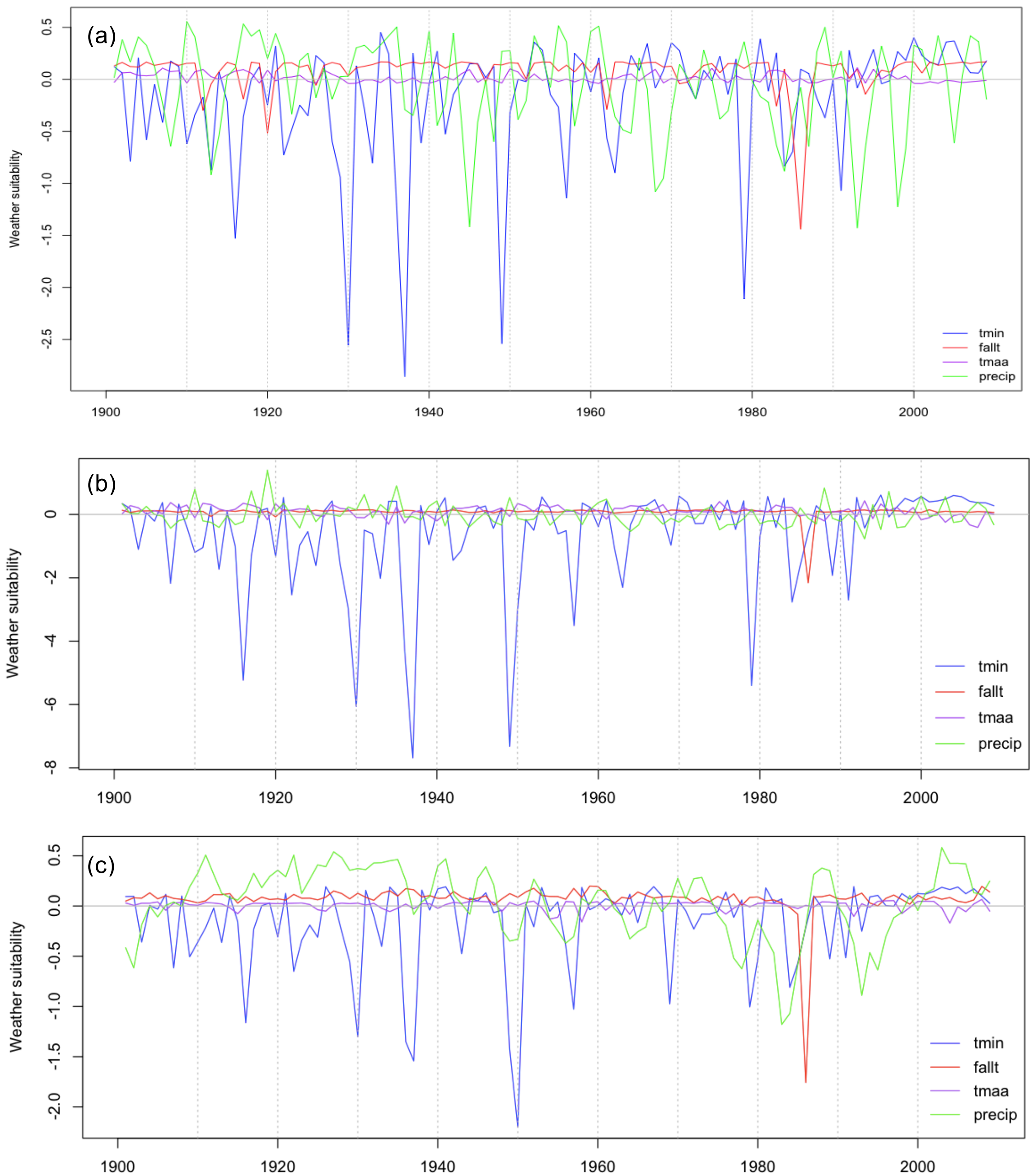


Figure S11. Spatially averaged suitability of individual weather variables from 1900-2009 calculated from the top model of probability of mortality from mountain pine beetles for the (a) Greater Yellowstone Ecosystem, (b) the Northern Rockies, and (c) the Cascades. See Table 1 for variable definitions.

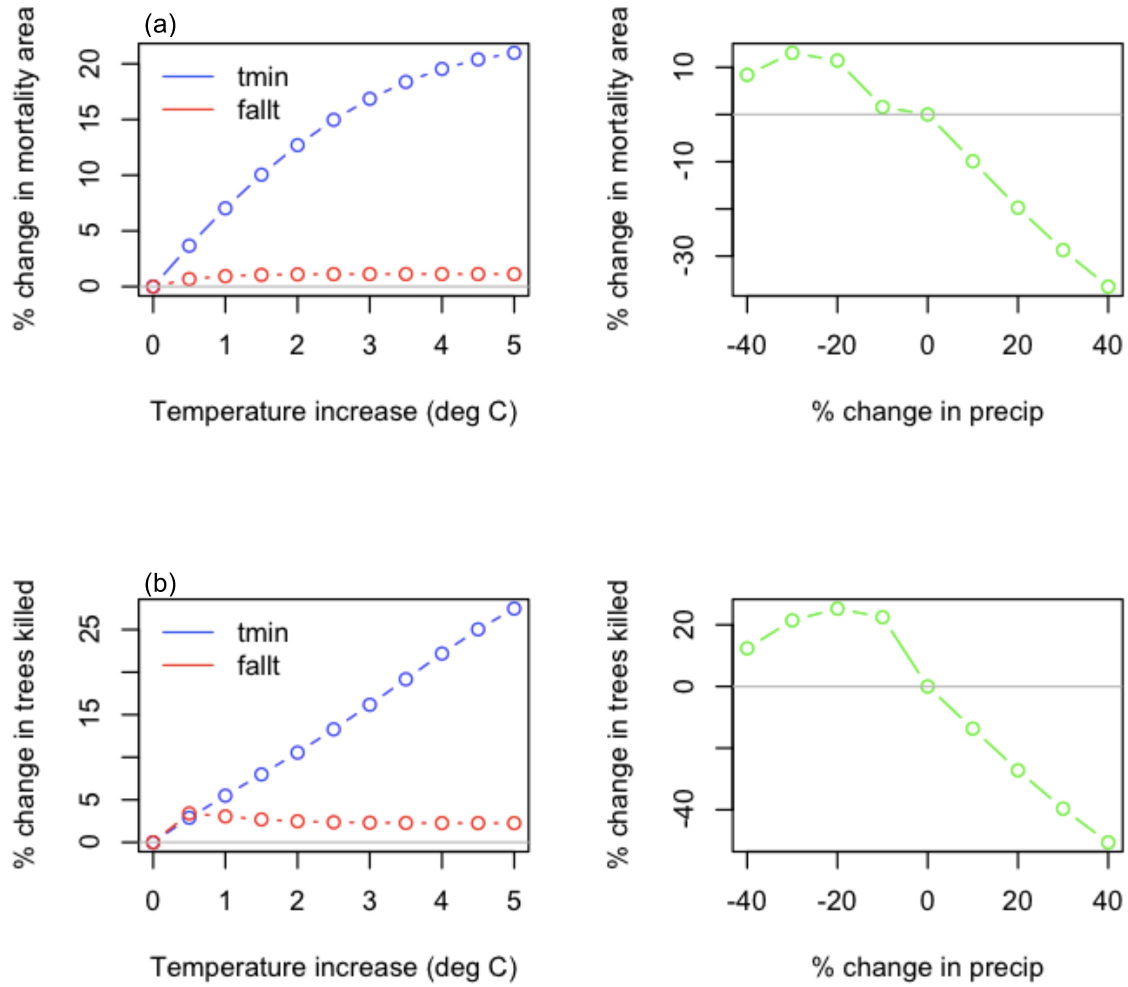


Figure S12. Climate change sensitivity in terms of (a) % change in mortality area relative to predicted mortality during 1998-2009 and (b) % change in total number of trees killed relative to predicted number of trees killed during 1998-2009 in the Greater Yellowstone Ecosystem. See Table 1 for variable definitions.

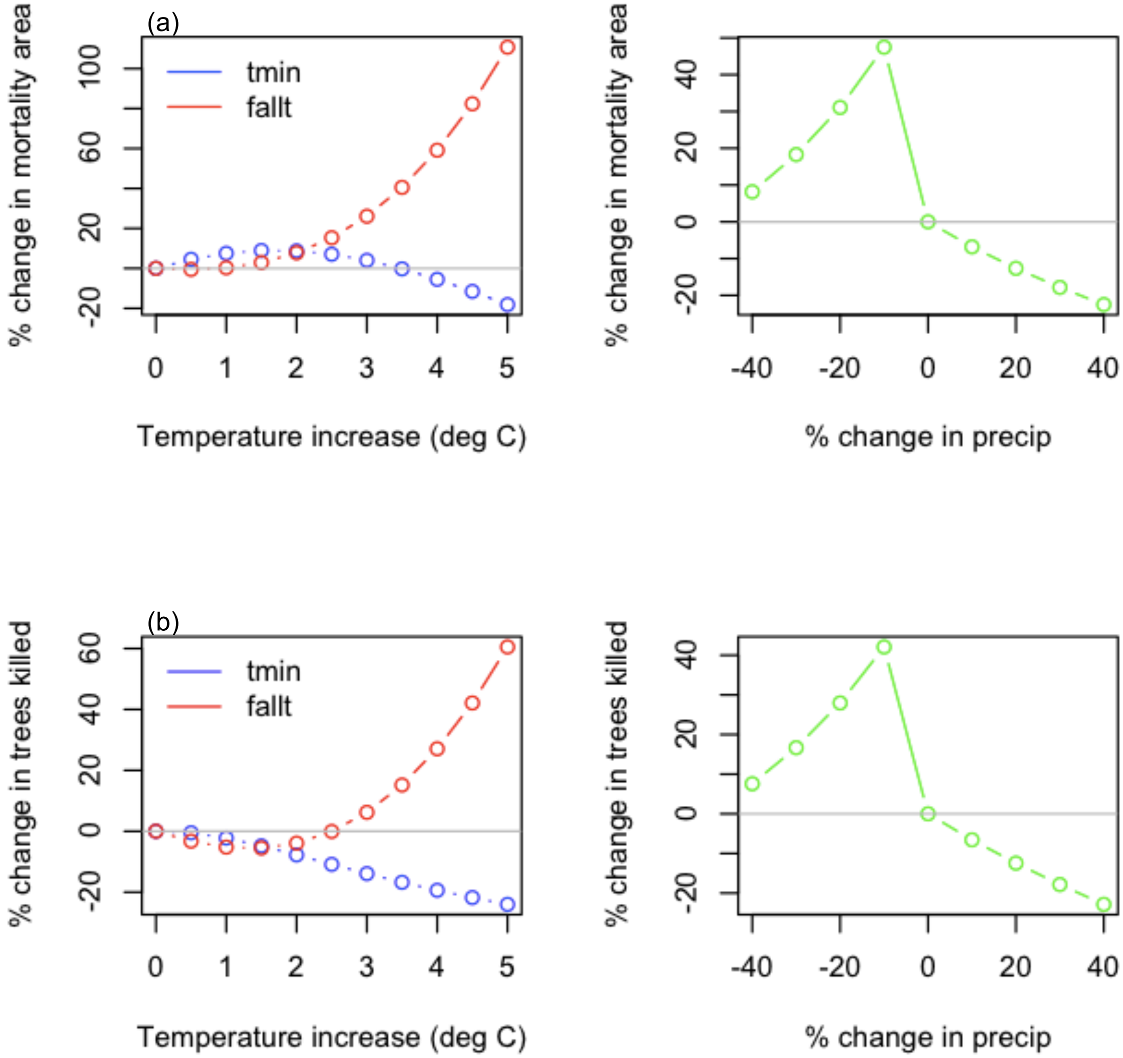


Figure S13. Climate change sensitivity in terms of (a) % change in mortality area relative to predicted mortality during 1998-2009 and (b) % change in total number of trees killed relative to predicted number of trees killed during 1998-2009 in the Northern Rockies. See Table 1 for variable definitions.

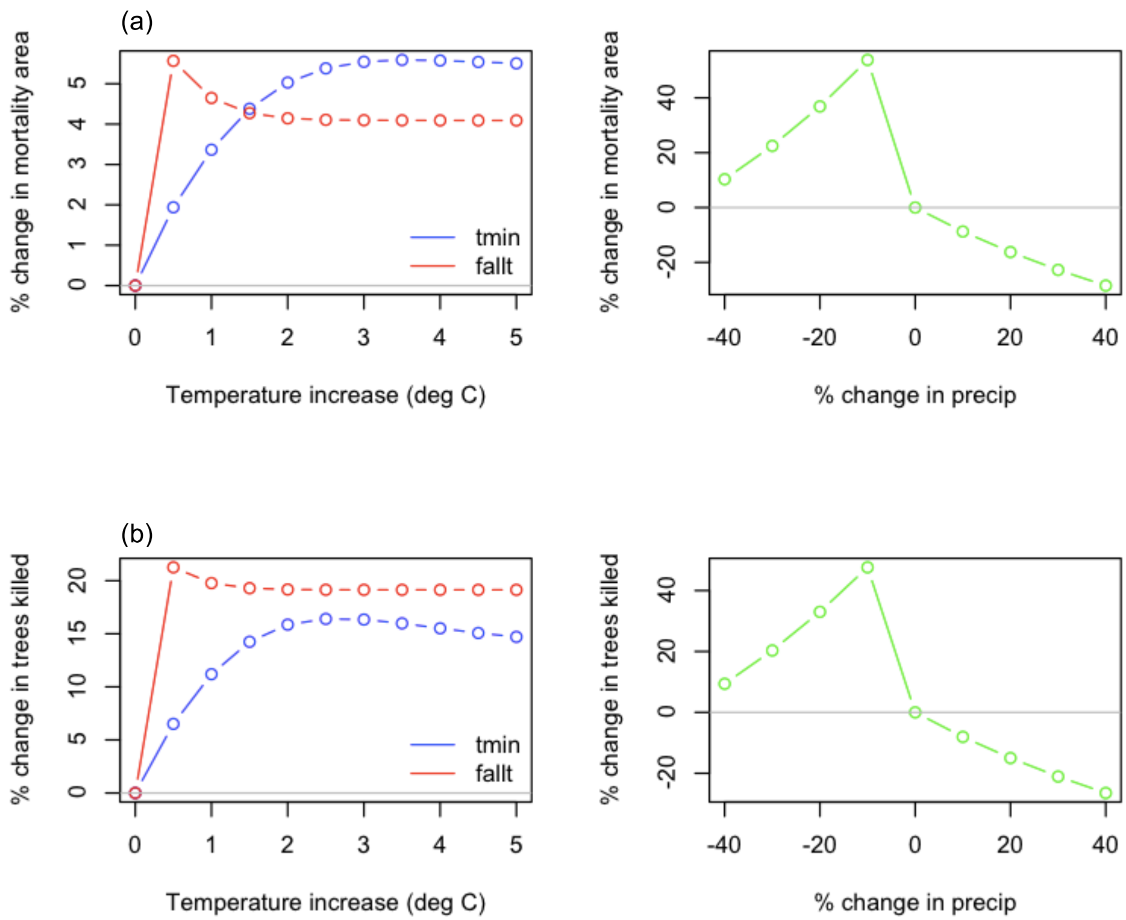


Figure S14. Climate change sensitivity in terms of (a) % change in mortality area relative to predicted mortality during 1998-2009 and (b) % change in total number of trees killed relative to predicted number of trees killed during 1998-2009 in the Cascades. See Table 1 for variable definitions.

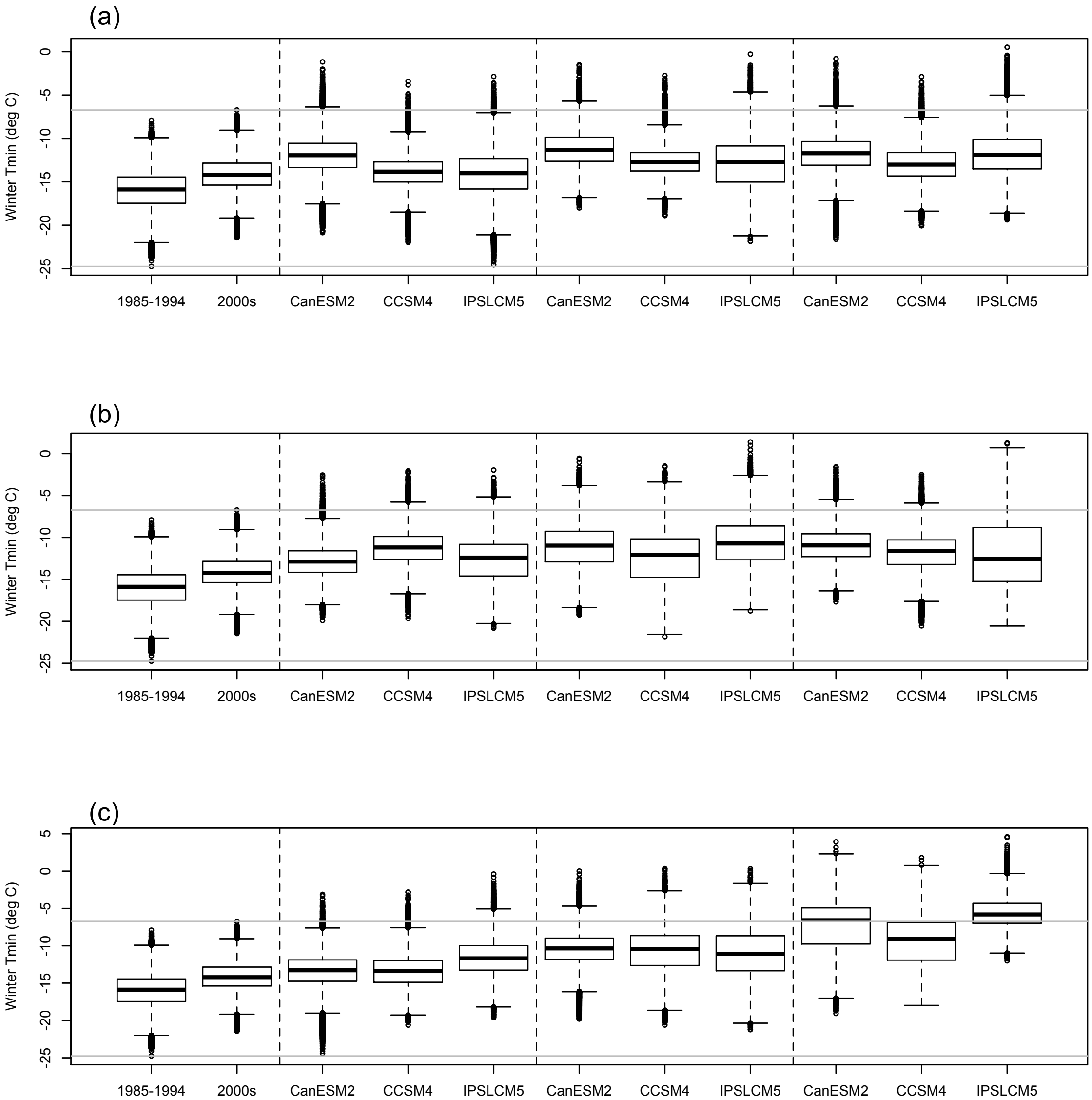


Figure S14. Preliminary results of comparison of winter minimum temperatures for a recent period without outbreaks (1985-1994), for the period of recent outbreak (2000s), and for climate change projections from three general circulation models (CanESM2, CCSM, IPSLCM5) and three future decades (2020s, 2050s, 2009s) for (a) RCP2.6, (b) RCP4.5, and (c) RCP8.5. Please check with authors for updates before using this figure.

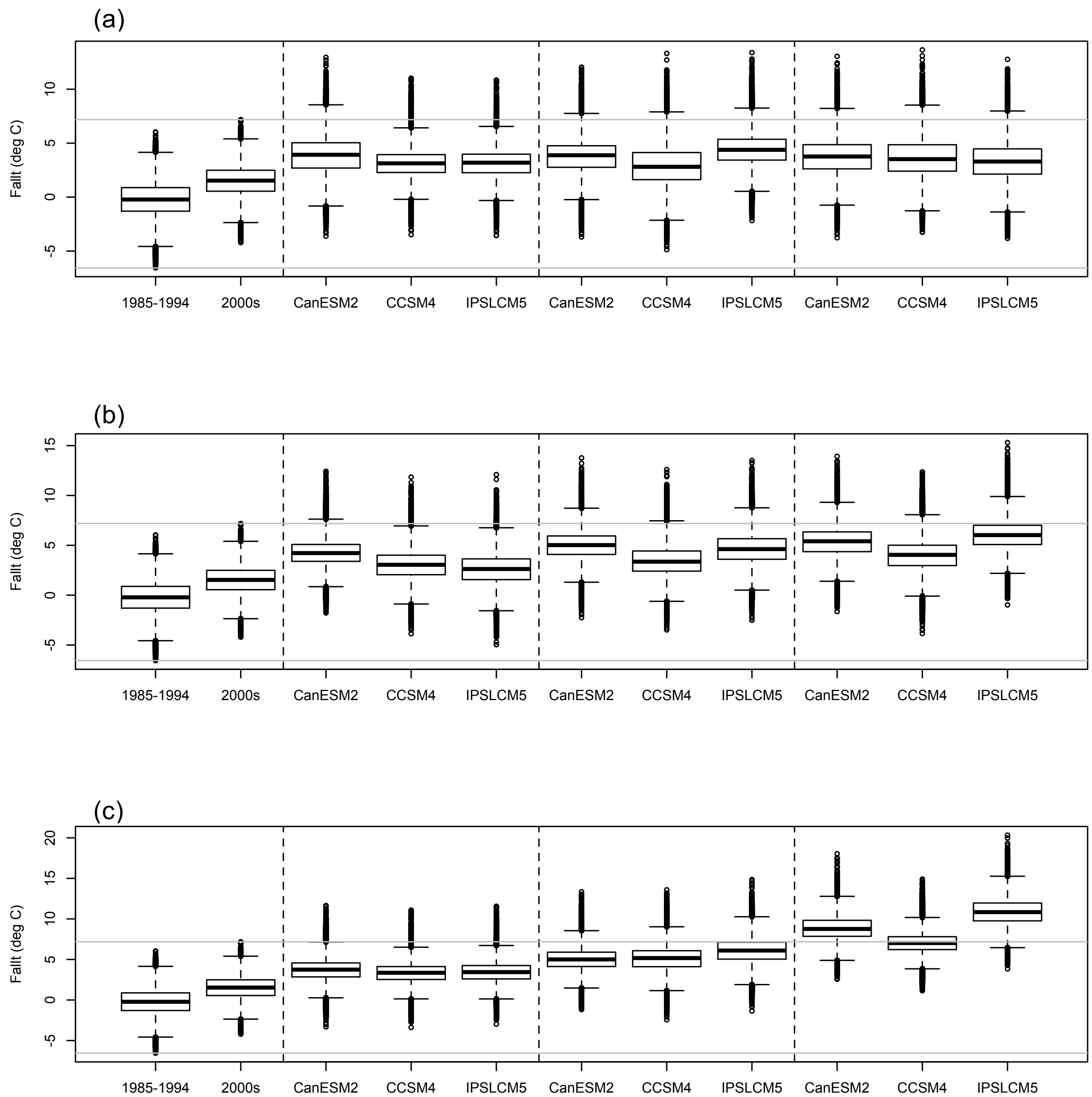


Figure S15. Preliminary results of comparison of fall temperatures for a recent period without outbreaks (1985-1994), for the period of recent outbreak (2000s), and for climate change projections from three general circulation models (CanESM2, CCSM, IPSLCM5) and three future decades (2020s, 2050s, 2009s) for (a) RCP2.6, (b) RCP4.5, and (c) RCP8.5. Please check with authors for updates before using this figure.

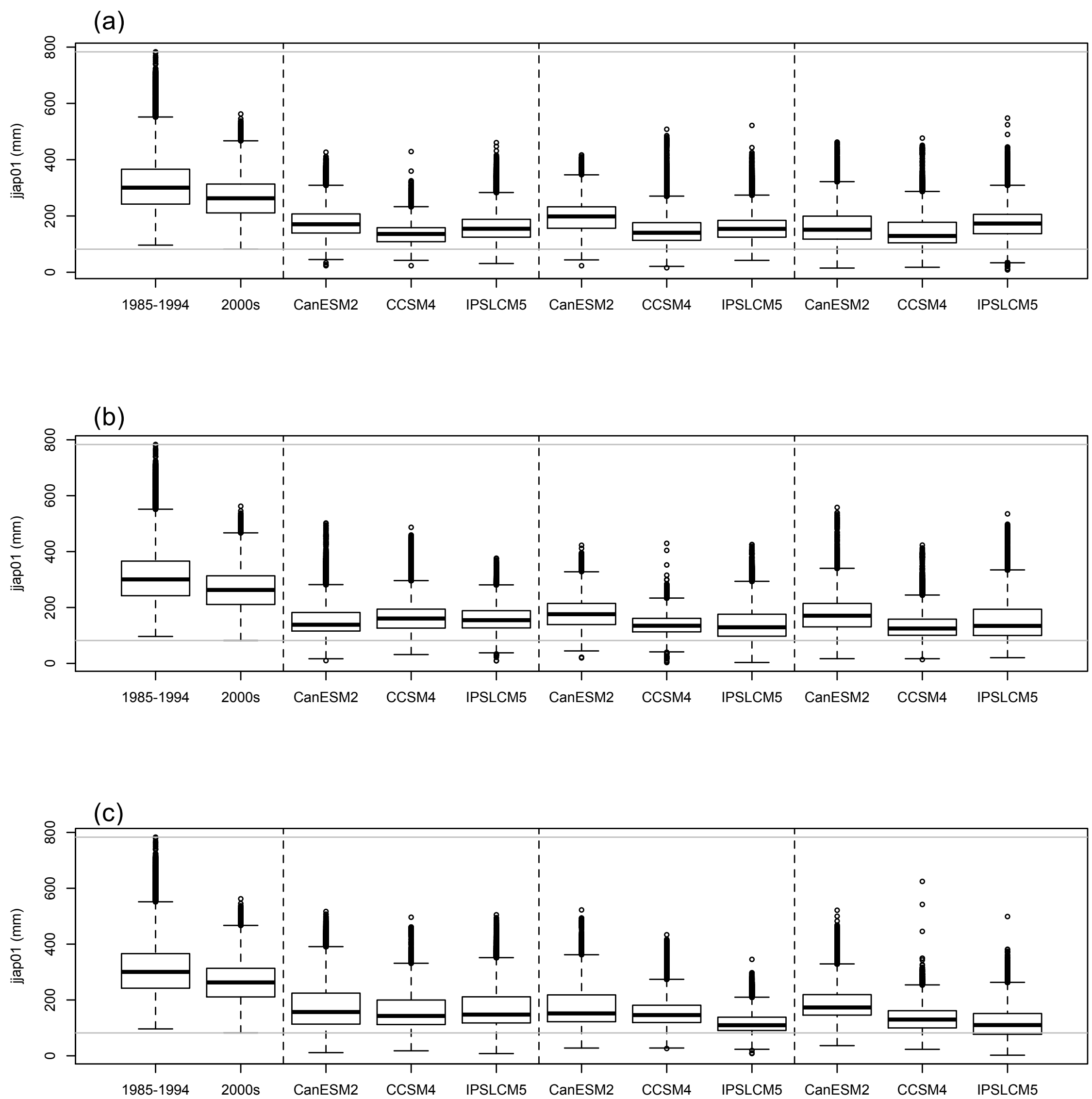


Figure S16. Preliminary results of comparison of June-July-August precipitation in the current and previous year for a recent period without outbreaks (1985-1994), for the period of recent outbreak (2000s), and for climate change projections from three general circulation models (CanESM2, CCSM, IPSLCM5) and three future decades (2020s, 2050s, 2009s) for (a) RCP2.6, (b) RCP4.5, and (c) RCP8.5. Please check with authors for updates before using this figure.